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STUDIES IN THE GENUS *COCCOLOBA*, V. THE GENUS IN HAITI AND THE DOMINICAN REPUBLIC

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IN VARIOUS LISTS of the flora of Hispaniola published by Lindau (the most recent monographer of the genus *Coccoloba*), Urban, Ekman, Barker and Dardeau (Flore d'Haiti 99-100. 1930) and Moscoso (Catalogus Florae Domingensis 168-171. 1943), forty-seven species and three forms of *Coccoloba* have been reported. Of these, thirty-two species and the three forms were considered to be endemic. Few of the species are either old or known only from the original collection or description. In general, the species are represented by several collections, the majority of which are the result of the meticulous collecting of Erik Ekman, who was encouraged by Ignatius Urban. There is no doubting Ekman's keen eye and inclusive memory for variations and locations. Again and again, his field notes indicate that he had seen the plant before and that it was the same as the earlier collection, or that a plant was different and "definitely not the same." Ekman's success in relocating old species or in collecting additional material was aided materially by his close co-operation with Urban. In many cases Urban directed Ekman to seek in a specific area which he designated from Berlin, or suggested that he look for a certain variation in an effort to recollect many of the older species. We are further indebted to them for retracing the routes of earlier botanists and for collecting sufficient new material to evaluate properly the older species. Ekman's collections were studied so promptly upon their receipt, that it appeared that the specimens were literally just received when Urban published a new name based on them. The rush to publish was continued after Urban's death by O. E. Schmidt who collaborated with Ekman, or rather, worked over his collections. Ekman's field notes indicate that he did not always agree with Schmidt and wished for more careful consideration of the entities involved.

Ekman recognized the general nature of the adventitious shoot in the genus *Coccoloba* and indicated in his field notes the variations from plant to plant and on single plants. Schmidt, in contrast, did not know the plants in the field and failed to appreciate Ekman's comments. As was indicated in an earlier study of the genus *Coccoloba* in Cuba (Jour. Arnold

Arb. 30: 388-424. 1949), Schmidt's failure to recognize adventitious shoots, the dioecious condition in the inflorescence and the nature of the pubescence led him to describe the two sexes of a single species under different names and to assign the adventitious shoots or the parent plants to different species, varieties or forms. Over a period of several years I have had the opportunity of spending several months collecting in the Dominican Republic and in Haiti.¹ During these collecting trips considerable emphasis was given to a field study of populations of the species of *Coccoloba*. I have made careful collections of young plants, mature plants, adventitious shoots and normal growth, as well as sun and shade foliage, to represent the range of leaf variation both on individual plants and in populations. Not all of the species reported from the island, or in fact, collected by Ekman, could be studied in the field. I believe, however, that the material which I have examined has made the conclusions drawn in this paper more reliable than the previously existing work.

I now recognize twenty-four species and four hybrid populations from Hispaniola. Fifteen species are regarded as restricted to the island. Three of the four hybrid populations are new but unnamed and, of these four hybrid populations, three are also to be considered endemic to Hispaniola, but may be expected on other islands. Of the fifteen endemic species, two (*Coccoloba fawcettii* and *C. ceibensis*) are regarded as representatives of probable hybrid populations. Two other species are questionably distinct from Cuban counterparts.

In addition to the fifteen endemic species, three (*Coccoloba costata*, *C. leonardii* and *C. wrightii*) are also known from Cuba but not from the Bahamas, Jamaica or Puerto Rico. Five species (*C. krugii*, *C. microstachya*, *C. pubescens*, *C. swartzii* and *C. venosa*) have ranges extending eastward throughout Puerto Rico to the Virgin Islands. Of these, *C. krugii* is also known from the Bahamas and from Jamaica and *C. swartzii* from Jamaica. *Coccoloba pubescens* and *C. venosa* have been reported from Jamaica but their occurrence there was questioned by me in an earlier paper (Jour. Arnold Arb. 38: 105-106. 1957). However, they are well known in Puerto Rico and the Lesser Antilles. Only two species (*C. diversifolia* and *C. uvifera*) are regarded as widespread in the Caribbean area, but further study may place *C. swartzii* in the same category. Hispaniola is indeed a center of speciation in the genus, but clearly not to the extent recognized by earlier authors.

The following key to the species is artificial and, unfortunately, for a

¹I am indebted to the trustees of the American Philosophical Society for a grant from the Penrose Fund which made one of these trips possible. I am also indebted to Mr. George Hamor of Hull's Cove, Maine, formerly of Barahona in the Dominican Republic, for his hospitality and assistance in the course of my field work. My appreciation is also gratefully expressed for the kindnesses and the co-operation given by many officials of the Dominican Republic; by the various officials of Compania Grenada of the United Fruit Company; by Dr. José de Js. Jiménez and Dr. M. Canela in services of value to this study. I am also grateful to the directors and curators of the herbaria cited in this paper for the long-term use of materials entrusted to their care when various aspects of this problem took extended time.

few species requires the use of complete material, including flowers and fruits. The majority of the species recognized are variable in vegetative characters, as an examination of the species descriptions will verify. The key given is applicable for all of the material which I have examined in fruiting condition and for most of the material when in flower. The key is not applicable in all cases to either sterile mature shoots or adventitious shoots. Abnormal variations on mature and adventitious shoots, such as fasciations, pathological anomalies and contortions have not been included in the key. Such specimens are common in herbaria and have been annotated, but are relatively infrequent in the field.

Many of the characteristics employed in the key should not be used in identification without considerable experience with the group. I have avoided the angles of departure of the primary veins which former monographers have used, but have used the prominence, curvature, bifurcations and reticulations of the primary and secondary veins individually or as patterns. I have introduced several new characters, such as the swelling of the nodes, the position of the base of the petiole in relation to the ocrea, the length of the pedicels in relation to the length of the ocreolae, the nature of the apex of the mature achene and the associated aspect of the lobes of the fruiting perianth. Morphological studies are needed on the bead-like swollen nodes which occur in a few species of *Coccoloba*. Swollen nodes are characteristic of the family Polygonaceae, but the exaggerated development of these in *Coccoloba* has not been investigated. The nodes are woody and extremely hard when dry. The pith in the swollen section is not enlarged. It is not clear whether the development of the nodal swelling is from the shortening of cambial initials or from a stimulated development of additional cells.

In most species of *Coccoloba* the petiole arises from the base of the ocrea. In a few species, the base of the petiole or the base of the abscission layer is a short distance above the base of the ocrea, as indicated both by vascular pattern and superficially by the color change between internodal stem tissue and the ocreal tissue. The relative position is readily determined in adventitious or vegetative shoots and can be seen on fertile specimens after the leaf has fallen. This characteristic has been checked in the field and appears to be a reliable one, since it shows no variation on individual plants or in populations.

In all but a very few species, the length of the pedicel is constant from the time the flower opens until the fruit is formed. The thickness of the pedicel varies, being much stouter when a fruit is developed than when the pistillate flowers do not form fruit. Staminate inflorescences show little thickening of the pedicels with age unless sterile fruits are produced.

The apex of the achene can be uniformly obtuse, acute, or constricted to form a rounded knob. When the last is the characteristic shape, the perianth in fruit consists of a fleshy hypanthium surrounding the body of the achene, the lobes of the perianth forming a crown around the knob. The latter condition has been referred to as "coronate." If the achene and the perianth are coronate, the perianth lobes may remain small and

free, or may become fleshy and imbricated around the knob. Since the crown is prominent very early, this character can be used on immature fruiting specimens, as well as on fully mature fruit. The prominence of the vascular supply in the fruiting perianth has been mentioned in the species descriptions but has not been used in the key to the species. The number of vascular bundles indicated in dry fruits as ridges and grooves seems to be a reliable indicator for a particular species. This characteristic must be verified when the fruit is dry and is, therefore, difficult to check in the field. The bundles are not evident when the fruit is fresh; however, species which later will have prominent bundles in the hypanthium are generally less fleshy and, therefore, less edible when sampled in the field. Since most species of *Coccoloba* which I have eaten have had extremely astringent fresh fruits, there is no particular pleasure in checking for this characteristic.

The number of flowers at each locus or node of the inflorescence is related to the functional sex of the flower. In most species studied, the functionally pistillate flowers are borne singly while the functionally staminate flowers are in clusters of two to five flowers. The number of flowers has been given unjustifiable emphasis by Lindau, Urban and Schmidt. I do not feel this should be used. Another characteristic used by Lindau in his keys was the condition of exerted versus included stamens. This, too, proved to be associated with functional or pollen-producing stamens, in contrast to the included sterile, rudimentary or abortive stamens. I have been unable to find any characteristics of diagnostic significance in the flowers of *Coccoloba* as the genus occurs in the West Indies. The flowers are small and variations in the size and shape of the floral parts appear to me to be too insignificant to be of real value.

Specimens are cited with standard abbreviations given for the herbaria as cited in the third edition of *Index Herbariorum*. The provinces cited for locations in the Dominican Republic are those used on the Esso Standard Oil Company "Mapa de la Republica Dominicana" prepared by the General Drafting Company and copyrighted in 1955. Province boundaries on this most recent map vary considerably from earlier maps available. The provinces are listed in alphabetical order. For Haiti, five departments are recognized and listed in geographic order from northwest to southwest. Navassa Island, formerly a United States possession, has been turned over to the government of Haiti and is considered as associated with the Département du Sud.

The species are described following the key and are listed in alphabetical order.

KEY TO THE SPECIES OF COCCOLOBA IN HISPANIOLA

- A. Perianth lobes exceeding the hypanthium in length, dominant in fruit; ocreolae increasing in size from flowering to fruiting condition; leaves chartaceous to membranaceous, rarely subcoriaceous.
- B. Leaves oblong-lanceolate to elliptic, longer than broad, apex acuminate. *C. venosa*.

- BB. Leaves orbicular to reniform, as broad as long, apex rounded to emarginate.
- C. Leaves of normal shoots 3×3 to 9×9 cm. long and broad; petioles arising from the base of the ocreae; inflorescence rachis 5–7 cm. long. *C. leoganensis*.
- CC. Leaves of normal shoots 0.2×0.2 to 1.1×1.0 cm. long and broad; petioles arising from above the base of the ocreae; inflorescence rachis 0.4–1.0 cm. long. *C. subcordata*.
- AA. Perianth lobes shorter than the hypanthium in fruit, imbricate or coronate; leaves generally coriaceous and not membranaceous.
- D. Leaves tipped with a spine or a cartilaginous point.
- E. Leaves cordate, the lower leaf surface with a conspicuous reticulum of veins. *C. fawcettii*.
- EE. Leaves ovate, oblong or elliptic, not cordate; lower leaf surface not conspicuously reticulate.
- F. Leaves oblong or elliptic.
- G. Primary veins 10–20 pairs, not raised on either surface and more or less uniform in strength; inflorescence rachis 1–4 cm. long; fruit rounded at the apex, not coronate, the base of the fruit attenuate but not sterile or corky; terminal spine of leaf 1 mm. long, sharp-pointed. *C. flavescens*.
- GG. Primary veins slightly elevated or evident below, 3–5 pairs; inflorescence rachis 5–15 cm. long; leaf blade terminated by a cartilaginous point, not sharp; fruit uncertain. *C. hotteana*.
- FF. Leaves ovate in general outline, broadest below the middle, venation evident and slightly raised on both surfaces; fruit coronate, the base sterile and corky.
- H. Primary veins generally 2–4 pairs, the lower two commonly separate from the others, the veins reaching to the margin before bifurcating and anastomosing; leaves generally 1–2 cm. long, uniformly acuminate from the middle to the apex. *C. incrassata*.
- HH. Primary veins generally 6–7 pairs, the lower two not noticeably separate from the others, the veins arcuate and bifurcating and anastomosing at a considerable distance from the margin; leaves generally 4–7 cm. long, the blade suddenly constricted above the middle and then acuminate to the apex. *C. fuertesii*.
- DD. Leaves not spine-tipped.
- I. Leaves with a conspicuous reticulum of raised veins and veinlets on the lower surface; perianth lobes imbricate in fruit, not coronate.
- J. Leaves of normal shoots 1–3 cm. long; inflorescence generally shorter than the leaves.
- K. Leaves of normal shoots as broad as or broader than long, apex rounded-truncate to emarginate. *C. picardae*.
- KK. Leaves of normal shoots longer than broad, apex apiculate to acuminate, rarely rounded but never subtruncate or emarginate. *C. pauciflora*.

- JJ. Leaves of normal shoots larger, 6×4 to 50×80 cm. long and broad; inflorescence generally exceeding the leaves.
- L. Leaves longer than broad; fruit ovoid.
- M. Leaves rounded and generally asymmetrical at the base with one lobe usually overlapping the petiole, the blade commonly bullate between the veins. *C. ceibensis*.
- MM. Leaves normally rounded and symmetrical at the base, occasionally cuneate, the blade not bullate. *C. wrightii*.
- LL. Leaves generally as broad as or broader than long.
- N. Fruit globose to ovoid; leaves generally pilose. *C. pubescens*.
- NN. Fruit obovoid, narrowed to a stalk at the base; leaves at most puberulent. *C. wifera* \times *C. pubescens*.
- II. Leaves without a conspicuous reticulum, primary veins alone conspicuous.
- O. Flowers and fruits sessile or the pedicels short and not exceeding the ocreolae in fruiting condition; perianth lobes coronate in fruit.
- P. Veins straight, not conspicuous, arcuate before bifurcating more or less equally and anastomosing near the margin; nodes swollen; petioles arising near the apex of the swollen nodes but from the base of the ocreae; leaves of normal shoots 3.5×5 to 7×4 cm. long and broad. *C. microstachya*.
- PP. Veins arcuate ascending, the terminal dichotomies unequal; nodes not conspicuously swollen or bead-like.
- Q. Petioles arising slightly above the base of the ocreae; fruits spindle-shaped, nearly twice as long as thick; leaf bases usually asymmetrical. *C. leonardii*.
- QQ. Petioles arising from the base of the ocreae; fruit globular to ovate, scarcely longer than broad.
- R. Leaves shiny when dry; fruit globular, 3 mm. diameter. *C. samanensis*.
- RR. Leaves dull when dry.
- S. Leaves of normal shoots obovate to obovate-elliptic, broadest above the middle, uniformly acute to rounded at the apex, not abruptly constricted; blade a dull brown when dry; fruit globular. *C. albicans*.
- SS. Leaves of normal shoots ovate to elliptic, broadest below the middle, usually abruptly narrowed above the middle and acuminate to the tip; blade turning black on drying; fruit ovoid. *C. swartzii*.
- OO. Flowers and fruits borne on pedicels which exceed the ocreolae in length.
- T. Leaves of normal shoots generally orbicular and as broad as long or broader.
- U. Branchlets with conspicuous swollen nodes, these often appearing moniliform.
- V. Leaves drying black; petioles arising from above the base of the ocreae; branchlets ferruginously pubescent. *C. nodosa*.

- VV. Leaves not turning black on drying; petioles arising from the base of the ocreae; branchlets pale puberulent. *C. buchii*.
- UU. Branchlets terete, the nodes not conspicuously swollen.
 - W. Perianth lobes and achene coronate in fruit.
 - X. Inflorescence rachis 1–2.5 cm. long. *C. buchii*.
 - XX. Inflorescence rachis 10–20 cm. long. *C. costata*.
 - WW. Perianth lobes imbricate in fruit, the achene not coronate.
 - Y. Leaves 6×8 to 13×18 cm. long and broad or larger; venation not conspicuous; fruit obpyriform, 1.2–2 cm. long. *C. uvifera*.
 - YY. Leaves 1.1×1.2 to 2.5×2.5 cm. long and broad; fruit 3–4 mm. long.
 - Z. Inflorescence rachis 0.2–0.5 cm. long; branches generally appearing to be arranged in one plane; venation of leaves reticulate and conspicuous on both surfaces when dry; fruit round in cross section. *C. picardae*.
 - ZZ. Inflorescence rachis 5–8 cm. long; branches geniculate, not appearing to be in one plane; venation inconspicuous on both surfaces when dry; fruit strongly 3-angled in cross section. *C. krugii*.
- TT. Leaves of normal shoots not orbicular, longer than broad.
 - a. Inflorescence rachis short, less than 3 cm. long.
 - b. Fruit coronate. *C. buchii*.
 - bb. Fruit not coronate, perianth lobes imbricate.
 - c. Leaves ovate, broadest below the middle, cordate at the base. *C. krugii*.
 - cc. Leaves obovate to obtriangular, broadest above the middle, narrowed or rounded at the base.
 - d. Leaves rounded-truncate to emarginate at the apex. *C. picardae*.
 - dd. Leaves normally apiculate to acuminate, rarely rounded but never subtruncate or emarginate at the apex. *C. pauciflora*.
 - aa. Inflorescence rachis normally 5–20 cm. long.
 - e. Flowering and fruiting pedicels short, exceeding the ocreolae but rarely twice as long.
 - f. Fruit sub-coronate at the apex; ocreae, petioles and rachises puberulent when young, the hairs generally persisting; leaves of normal shoots generally 7×5 cm. long and broad or larger; blades dark green when fresh and golden to dark brown when dry. *C. costata*.
 - ff. Fruit not coronate at the apex; ocreae, petioles and rachises glabrous; leaves of normal shoots generally

- 4 × 3 cm. long and broad or smaller; leaf blades pale greenish-tan in color when fresh or dry. *C. krugii*.
- ee. Flowering and fruiting pedicels conspicuous, two to several times the length of the ocreolae.
- g. Perianth lobes and achene sub-coronate when mature; primary veins of leaves conspicuous and with secondary venation forming an elevated and conspicuous reticulum on both surfaces when dry. *C. wrightii*.
- gg. Perianth lobes imbricate, the achene rounded at the apex, not sub-coronate; primary veins evident, secondary venation inconspicuous, not elevated and reticulated on the lower surface.
- h. All parts glabrous. *C. diversifolia*.
- hh. Ocreae, petioles and inflorescence rachises puberulent or pubescent at least when young. *C. hotteana*.

Coccoloba albicans Ekman in Schmidt, Fedde Rep. Spec. Nov. 27: 103. 1929.

Small, medium or large tree (fide Ekman); branches terete, striate or canaliculate, light gray, glabrous; ocreae 6–8 mm. long, stiff, glabrous, cleft at the apex, frequently splitting at maturity and appearing as two ovate-lanceolate acuminate stipules; leaves of normal shoots with petioles 4–6 mm. long, glabrous, arising from the base of the ocreae; blades obovate to obovate-elliptic, 4 × 2.5, 5 × 4, to 5.5 × 3.5 cm. long and broad, coriaceous, glabrous, the apex rounded, rarely bluntly apiculate, the base rounded, the margin slightly revolute; midrib and primary veins impressed above, prominent below, the primary veins 6–8 pairs, arcuate, anastomosing conspicuously near the margins, the ultimate venation evident below but not above; leaves of adventitious or fast-growing shoots with ocreae 1–1.5 cm. long, the petioles 1–1.2 cm. long, the blades obovate-elliptic to elliptic-lanceolate, rarely ovate-elliptic, 6.5 × 5, 8.5 × 6, to 9.5 × 5 cm. long and broad, otherwise the same; inflorescences single or aggregated as 3 or 4 racemes, terminal or terminal on axillary shoots, to 13 cm. long, the basal ocreae to 1 cm. long, the rachis angular, glabrous; flowers sessile, the staminate flowers 1–3 at each locus, the pistillate flowers 1 at each locus, the bracts about 0.5 mm. long, ocreolae membranaceous, 1–1.5 mm. long, expanding and splitting after flowering; hypanthium to 1 mm. long, the perianth lobes ovate to suborbicular, 1.8 × 2.0 mm. long and broad, the functional stamens 1–1.5 mm. long, the rudimentary stamens less than 0.5 mm. long, the fertile pistil 2.5 mm. long, the ovary triangular, the rudimentary pistil about 0.5 mm. long; fruit sessile, ovoid to globose, 5 mm. long, 4.5–5 mm. in diameter, the perianth lobes slightly coronate, the achene light tan in color.

DISTRIBUTION: Endemic to Haiti.

Haiti. DEPT. DU SUD: Massif de la Hotte, Les Roseaux, Nan-Patates, Ekman H-10693 (s-lectotype, us); Les Roseaux between Nan-Patates and Alnette, Ek-

man H-10720 (B, S); Massif de la Hotte, Morne Rochelois, Miragoâne at Quaert-Chemis, *Ekman* H-9206 (S), H-7936 (A, S, US); Miragoâne on trail to Morne Rochelois, *Eyerdam* 515 (F, GH, NY, US), 519 (A, F, GH, NY, US).

It is not clear to me whether Schmidt or Ekman compiled the original description of *Coccoloba albicans*. Although the species was published by Schmidt, he gives credit to Ekman for the taxon as a new entity. Various herbarium sheets bear labels indicating as author either Ekman or Ekman and Schmidt. In any case, leaves from fast-growing shoots and those from shoots of normal growth have been combined in the description, with a resulting lack of clarity. The description above distinguishes between the branches which are mature and those which are terminal shoots or adventitious branches. Among the specimens cited are both flowering and sterile adventitious shoots.

The original publication cites *Ekman* H-10693 as the type. However, the collection 10720 in the Berlin herbarium bears the annotation "typus" in Urban's handwriting, while the Stockholm specimen of the same number has a printed label indicating that is the type. A specimen of the number published as the type is not in the Berlin herbarium and I have chosen to select the Stockholm specimen of *Ekman* H-10693 as a lectotype. This is the correct number as published and is better material than is the second collection cited in the original description and labeled as the type.

Two collections, *Ekman* H-7936 and H-9206, were originally labeled "*Coccoloba albicans* Ekman, forma." These are the smaller-leaved mature branches, while the collection *Ekman* 10720 labeled "typus" by Schmidt consists primarily of adventitious shoots.

The collections cited in the original publication are from staminate plants. The collection *Ekman* H-7936 labeled "forma" bears fruit. Pistillate flowers are seen on the *Eyerdam* collections. In the original description Schmidt refers to the punctations on the lower leaf surface. These are blocked stomata and their adjacent cells which dry darker than other areas of the lower mesophyll.

Coccoloba buchii Schmidt, Ark. Bot. 20A(15): 32. 1926; Fedde Rep. Spec. Nov. 24: 75. 1927.

Coccoloba revoluta Leonard, Jour. Wash. Acad. Sci. 17: 66. 1927.

Coccoloba tortuensis Ekman & Schmidt, Ark. Bot. 20A(15): 32. 1926.

Coccoloba ciferriana Ekman, Bull. Estac. Bot. Moca, Ser. B, 17: 10. 1927 (nomen).

Small tree with numerous spreading branches; branches terete, puberulent to pilose, the nodes slightly tumid; ocreae membranaceous, 3–7 mm. long, oblique to nearly bilobed at the apex, puberulent to pilose; leaves of normal shoots with petioles 3–4 mm. long, puberulent to pilose, at least on the adaxial surface, arising from the bases of the ocreae, the blades ovate to elliptic-orbicular or reniform to obovate-elliptic, 2×1.5 , $3 \times 2 \frac{1}{2}$ cm., thin, coriaceous, puberulent above, glabrous below, the apex

rounded or obtuse, the base subcordate, rounded or occasionally narrowed, the margin entire, recurved; midrib prominent on both surfaces, the primary veins 5 or 6 pairs, straight or slightly arcuate, strongly recurved and anastomosing near the margin, the secondary venation minutely reticulate above, coarsely reticulate below; leaves of adventitious shoots with petioles 4–5 mm. long, the blades elliptic, elliptic-lanceolate to ovate-lanceolate, 4.5×3 , 8.5×3 to 11.5×4.5 cm. long and broad; inflorescences terminal on short lateral shoots 1–2.5 cm. long, the rachis puberulent at the base or on the lower portion, becoming glabrate; staminate flowers 1–3 at each locus, pistillate flowers borne singly at each locus, the bracts and ocreolae membranaceous, to 1 mm. long, the ocreolae tightly cylindrical around the pedicels, the hypanthium less than 1 mm. long, the perianth lobes ovate, 1 mm. in diameter, the fertile stamens to 1 mm. long; fruiting pedicels 1–1.5 mm. long, glabrous, the fruit ovoid, 5 mm. long, 4 mm. in diameter, the base rounded, the perianth lobes subcoronate, the achene brown.

LOCAL NAME: *Papelite* (H).

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. INDEPENDENCIA: near Puerto Escondido, *Howard 12150* (GH). PROV. LIBERTADOR: between Restauración and Banica, *Howard 12554* (GH). PROV. MONTE CRISTI: El Morro, *Ekman 13140* (A, s, us, number designated by Ekman and Schmidt as type of *Coccoloba ciferriana*), *Howard 12533* (GH), *Howard 12535* (GH), *Jiménez 1370* (GH). PROV. PUERTO PLATA: Arroyo Francés, *Ekman 14399* (s, us). PROV. SAMANÁ: Los Haitises, Boca del Infierno, *Ekman 15439a* (s), *15439b* (s, us), *15439c* (s), *15439d* (s). PROV. SANTIAGO: Las Lagunas at Arroyo Arrenquillo, *Ekman 16078* (s).

Haiti. DEPT. DU NORD OUEST: Moustique Mts., Bassin Bleu, *E.C. & G.M. Leonard 15235* (NY, us), Port de Paix, *Ekman H-3646* (B, s, us), Presqu'île du Nord-Ouest, Port de Paix, Haut Moustique, *Ekman H-3647* (s), Isle de la Tortue, La Vallée, Morne Barranca, *Ekman H-4107* (b-type of *C. tortuensis*, s, us), *H-4308* (B, s). DEPT. DU NORD: St. Michel de l'Atalaye, *E.C. Leonard 8499* (B, GH, us-type of *C. revoluta*), *7244* (NY, us), Massif du Nord, Gros Morne, Morne Chabre, *Ekman H-5024* (s), Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4951* (s-type of *C. buchii*).

Ekman in his publication entitled "Excursion Botanica al Nord-Oeste de la Republica Dominicana" (Estacion Agronomica de Moca, Ser. B. 17: 9–10. 1930) refers to a new and distinct species of *Coccoloba* on the top of El Morro near Monte Cristi. He comments that this is dedicated to his amiable companion of the trip, Dr. R. Ciferri. His field label for this specimen (*Ekman 13140*) reads "*C. Ciferriana* Ekman." Later collections from neighboring areas, e.g., *Ekman 14399*, from Arroyo Francés near Puerto Plata, and *Ekman 16078*, Arroyo Arrenquillo near Santiago, all bear field labels reading, "*C. Ciferriana* Ekman and Schmidt." By 1932, however, Schmidt had changed his opinion of this material and all the sheets cited above bear his annotation labels reading "*Coccoloba Buchii*."

A study of these plants in the field reveals that both *Coccoloba buchii*

as interpreted by Schmidt and *C. ciferriana* as interpreted by Ekman are present on the top of El Morro. Careful analyses of these populations were made in the field and reveal a continuous variation in a series in the shape of the leaves from sterile and fertile plants and from normal leaves to leaves of adventitious shoots. The type specimens chosen for these species (and for *C. revoluta*) represent extremes of the variation. It is more satisfactory to consider the entire range of variation as delimiting the species and to apply the oldest name, *C. buchii*, to the population. *Coccoloba revoluta* Leonard represents an extreme development of pubescence.

The assignment to this species of plants from the Samaná Peninsula in eastern Hispaniola extends the range of the species to the eastward, in violation of Ekman's concepts of species distribution in Hispaniola. Ekman's field label for his collection 15439 is preserved in the Stockholm herbarium. He believed that this plant from the Bocas del Infierno in Samaná was a new species having affinities with *C. flavescens*. He commented, "The plants made, however, the impression of something new. The leaves of the saplings are larger than those of mature plants, otherwise similar." To this Ekman added "a,b,c,d, different stages, a — mature, d — sapling." All of these specimens are sterile and *Ekman 15439a*, described by Ekman as a mature shrub, has smaller ovate-elliptic leaves 4.5×3 to 3.5×2 cm. long and broad. Specimens 15439 c & d are obviously from faster-growing leader or adventitious shoots. The leaves of these are lanceolate-ovate to 7.5×2 cm. long and broad to elliptic-ovate 10×4 cm. long and broad. It seems best to recognize this as a normal variation, although a troublesome one from the taxonomic point of view.

Howard 12554 is tentatively referred to this species. The flowers were either past or else the inflorescence had aborted in the dry period. Leaves of the adventitious shoots are larger, thicker and more prominently veined than in the remainder of the specimens seen in the field or cited above.

Coccoloba tortuensis was based on *Ekman H-4107* and *H-4308*, the former being selected by Schmidt as the type. It was described at the same time as *C. buchii* and both species were based on incomplete or sterile material. In subsequent papers Schmidt referred additional specimens to *C. buchii* and expanded his definition of this species. It is my feeling that *C. tortuensis* should be referred to the synonymy of *C. buchii*. Originally Schmidt distinguished between *C. buchii* and *C. tortuensis* on the basis of the length of the ocrea, the size of the leaf and thickness of the nodes and the leaf shape. In all characters considered, *C. tortuensis* is sufficiently similar to *C. buchii* to be referred to it. The leaf shape is slightly different and the pubescence on young parts heavier, but these are within the range of expected variation.

Coccoloba buchii is similar in general appearance to *C. praecox* of Cuba, especially in sterile condition. The two species can be distinguished on the basis of the more tumid nodes, the longer inflorescences, the larger leaves and petioles of *C. praecox*.

Coccoloba krugii is also similar to *C. buchii*, but the former can be distinguished by the more cordate-ovate leaves, the angular rachis of the inflorescence and the angular fruits.

Coccoloba ceibensis Schmidt, Fedde Rep. Spec. Nov. 32: 81. 1933.

Shrub or small tree; branches terete, striate, puberulent, the nodes swollen; ocreae 1–1.5 cm. long, uniformly membranaceous, ferruginous puberulent, bilobed and acute at the apex; leaves with petioles 5–7 mm. long, puberulent, attached at the bases of the ocreae; blades broadly elliptic, to ovate-elliptic or obovate-elliptic, 7×5 , 10×8.5 , 12×10 cm. long and broad, coriaceous, slightly bullate especially between the veins, the apex rounded to apiculate, the base rounded, the margin recurved; midrib slightly impressed but sharply keeled above, prominent below; primary veins 6–8 pairs, arcuate and anastomosing near the margin, impressed above and conspicuous below, the ultimate venation also conspicuous below, the lower leaf surface sparsely short pilose-pubescent, the upper surface glabrous and pitted; inflorescences terminal, 8–11.5 cm. long, the basal ocreae to 1.5 cm. long, puberulent, the rachis angular, puberulent; flowering material not known; fruiting racemes with broadly triangular bracts to 1 mm. long, the ocreolae 1–1.2 mm. long, the fruiting pedicels 1–1.5 mm. long; fruit ovoid, 6 mm. long and 4 mm. diameter, the perianth lobes half the length of the fruit, imbricate, the achene tan to brown, shining.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. TRUJILLO: Llano Costero, Cuenca at La Ceiba, *Ekman H-13344* (b-type, s); Llano Costero, El Manielito, *Ekman H-14281* (s); Bayaguana at Loma Managuá, *Ekman H-11108* (s).

Material of *Coccoloba ceibensis* has not been recollected in satisfactory condition and the species is known only from the type collection. The two additional Ekman collections cited above are referred here but with some question. *Ekman H-11108* was collected in sterile condition in January, 1929. The second collection, *Ekman H-14281*, was collected in February, 1930, and Ekman states on his field notes, "collected before sterile." Schmidt noted this comment with his initials and a question mark. The second collection is fragmentary, consisting of two small branchlets, in quality unlike the material Ekman generally prepared. It bears a staminate inflorescence. Schmidt referred this specimen to *C. scrobiculata*, a species which I have referred to *C. wrightii*. Schmidt compared this species with *C. pubescens*, as well as with *C. jawcettii*, which I have suggested represents the hybrid of *C. pubescens* and *C. fuertesii*.

Coccoloba ceibensis appears to me to be a hybrid of *C. pubescens* and probably *C. samanensis*, although the latter species has not been reported from the same area. The strong venation of the leaves and the shape of the fruit with the imbricated lobes of the perianth are similar to *C. pubescens*. The suggested parentage of *C. samanensis* is based on the short fruiting

pedicels surrounded by membranaceous ocreolae, as well as the texture and aspect of the upper leaf surface. Although I spent some time collecting in the area where Ekman found these plants, I was unable to locate additional material near stands of *C. pubescens*. Ekman reported on the field label of the type specimen that the plant was "not common."

Coccoloba costata Wr. ex Sauvalle, Fl. Cub. 139. 1868; Lindau, Engl. Bot. Jahrb. 13: 155. 1890, Symb. Antill. 1: 225. 1899; Schmidt, Fedde Rep. Spec. Nov. 27: 105. 1929; Howard, Jour. Arnold Arb. 30: 145. 1949, 38: 235. 1957.

Coccoloba eggersiana Lindau, Engl. Bot. Jahrb. 13: 153. 1890.

Coccoloba verruculosa Lindau, Engl. Bot. Jahrb. 13: 154. 1890.

Coccoloba rupicola Urban, Symb. Antill. 6: 10. 1909.

Coccoloba sp. Urban, Symb. Antill. 4: 656. 1911.

Coccolobis costata Brit. & Wils. Sci. Surv. P. R. 5: 270. 1924.

Coccoloba helwigii Schmidt, Fedde Rep. Spec. Nov. 27: 104. 1929.

Coccoloba samuelssonii Ekman & Schmidt, Fedde Rep. Spec. Nov. 27: 105. 1929.

Small tree of shrubby growth or tree to 30 feet tall; branches stout with a ferruginous to golden pubescence, this often persisting only in protected spots or at the apex; ocreae membranaceous 4–6 mm. long, ferruginous-puberulent to subglabrous; leaves of normal shoots with petioles 8–10 mm. long, stout, lightly puberulent, arising from the bases of the ocreae; blades generally ovate to elliptic, less commonly suborbicular to obovate-orbicular, 2.5×2.2 , 5×5 , 7×5 , 11×8 , to 18×12 cm. long and broad, coriaceous, usually golden, shining above, dull brown below, sparsely pitted above and below, often showing anomalous peltate or variously shaped resinous stomatal excretions which may be black and are abundant when the leaf is young, scattered and few in mature leaves, otherwise glabrous; apex obtuse or rounded, the base generally slightly and unequally cordate to narrowly and unequally decurrent on the petiole; midrib and veins impressed above, prominent below, the primary veins 5–7 pairs, arcuate, anastomosing; leaves of adventitious shoots to 35×22 cm. long and broad on petioles to 1.5 cm. long; inflorescence terminal, rachis puberulent, 15–20 cm. long, the staminate flowers in clusters of 2–4, the pistillate flowers solitary on pedicels 0.5 mm. long, the bracts ovate, 0.5 mm. long, the ocreolae membranaceous, 0.5 mm. long, the hypanthium 0.5 mm. long, the perianth lobes 0.5–1 mm. long and broad, the fertile stamens 1 mm. long; fruiting pedicels to 1.5 mm. long, the fruit globose to 6 mm. long, 5 mm. thick, the perianth lobes coronate.

DISTRIBUTION: Cuba, Hispaniola, Puerto Rico.

Dominican Republic. PROV. BARAHONA: Palo Mino to Montasse on trail to Polo, Howard 12070 (GH), 12233 (GH); Mt. Laho, La Cueva to Placer Bonito, Howard 12272 (A, GH). PROV. BENEFACTOR: San Juan, Loma La Vieja near Lemba, Ekman H-13448 (S, US); Rio Arriba del Norte, Howard 8843 (GH). PROV. LA VEGA: Banao, Firme del Banilejo, Ekman H-16460 (S, US). PROV.

PUERTO PLATA: La Rosa, *Eggers 1762* (b-type of *C. verruculosa*, K, M, NBV); Sosúa, *Ekman H-14459* (s); Puerto Plata, *Eggers 2731* (b-type of *C. eggersiana*, GH, M), *Ekman H-14401* (A, s). PROV. TRUJILLO: Villa Altagracia, *Ekman H-11231* (s).

Haiti. DEPT. DU NORD OUEST: Bombardopolis, *EC & GM Leonard 13509* (NY, us). DEPT. DU NORD: Massif du Nord, Le Borgne, edge of Estere Savate, *Ekman H-4855* (b-type of *C. samuelssonii*, s, us); Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4944* (s, us), *H-8523* (b-type of *C. helwigii*, s); Massif du Nord, Hinche, Bois Charles, *Ekman H-6077* (s, us); Massif du Nord, Bayeux, Morne Brigand, *Ekman H-2855* (b, s, us); Massif du Nord, St. Louis du Nord, Morne Baron, *Ekman H-4684* (s); Massif du Nord, St. Louis du Nord, between Baron and Rio Jean-Claire, *Ekman H-3904* (s). DEPT. DE L'OUEST: Massif des Matheux, l'Archaie, Lully to Caye-Nicolas, *Ekman H-9287* (A, s, us); Massif des Cahos, Las Caobas, Belladère, *Ekman H-5589* (b, s); Ile de la Gonave, *Ekman H-8721* (s).

In a treatment of the genus *Coccoloba* as it occurs in Puerto Rico (Jour. Arnold Arb. 38: 235-237. 1957), I discussed the morphological variation of *Coccoloba costata* and extended the recognized range of this species from Cuba alone to Hispaniola and Puerto Rico. A number of species from Hispaniola formerly considered distinct and endemic were reduced to the synonymy of this taxon. These included *C. samuelssonii*, considered distinct on the shape of the leaf base and the texture and shine of the leaf blade; *C. helwigii*, supposedly distinct in having orbicular leaves with minute punctations, the latter proving to be blocked stomata and resinous excretions from the stomata; and *C. verruculosa* which Lindau distinguished from *C. costata* on the matter of pubescence as well as the number and length of flowering pedicels. Still another Hispaniolan endemic species, *C. eggersiana*, must be included in this species and reduced to the synonymy of *C. costata*. In his key Lindau distinguishes *C. eggersiana* from *C. verruculosa* by the size of the leaves and the thickness of the inflorescence rachis. *Coccoloba eggersiana* is also distinguished from *C. costata* in the same key on the absence of pubescence on the inflorescence rachis. The abundance of material cited above demonstrates numerous intermediates on all characters and the type collection of *C. samuelssonii* (*Ekman H-4855*) shows clearly the range of variation from material matching the type of *C. costata* to shoots comparable to the type specimens of *C. eggersiana*.

The following series of specimens from near Puerto Plata and from the Province of Samaná are referred to *Coccoloba costata*, but with some question: PROV. PUERTO PLATA: Sosúa, coral reef at Forma, *Ekman H-14460* (s, us). PROV. SAMANÁ: San Lorenzo Bay, *Abbott 2237* (b, GH, NY, us); 2245 (us); Samaná, Laguna, *Ekman H-15096* (s, us); Los Haitises, Cueva de Cal, *Ekman H-15573* (s); Samaná, Laguna, Loma Zaramagua, *Ekman H-15249*; Los Haitises, Cayo de los Cueros, *Ekman H-15516* (s).

Each of these collections differs in some aspect from the expected range of variation now recognized for *Coccoloba costata*. Two collections, *Ek-*

man 14460 and *15096*, from Puerto Plata and Samaná respectively, have normal shoots with leaves similar to the type specimen of *C. eggersiana* and are clearly confluent with the range and variation of *C. costata*. The adventitious shoots of these same plants which are mounted on herbarium sheets are oblong, varying from 7.5×3 to 14×4.5 cm. long and wide. This leaf shape has not been found on adventitious shoots of *C. costata* in other sections of its range. *Ekman 15249* and *15573* from the Samaná peninsula and the two Abbott collections from the same area appear to be vigorous shoots, possibly adventitious in origin, but with small oblong leaves 6×2 to 9×2.5 cm. long and wide. All of these collections bear staminate inflorescences. *Ekman 15573* bears field notes indicating that the plant is "very common in the Haitises." It also has unripe fruits which are too small to permit the determination of either the fertility of the fruits or their possible similarity to those of *C. costata*. Finally, *Ekman H-15516* from Los Haitises bears a staminate inflorescence and unripe fruits which appear to be comparable to those of the Ekman collection just mentioned. This plant, Ekman notes on his field label, is "rare" in the same area. The leaves of collection *H-15516* are ovate-lanceolate to lanceolate-oblong. While the leaf base is similar to that expected in *C. costata*, the general aspect of this specimen suggests a relationship to *C. diversifolia*. It is possible that further collections may reveal a hybrid population of *C. diversifolia* and *C. costata* in the Samaná area, particularly inland on the limestone mountains.

***Coccoloba costata* Wr. ex Sauv. \times *Coccoloba uvifera* L., hybr. nov.**

Shrub or small tree (acc. Ekman), branches terete, striate; persistent bases of ocreae 4–5 mm. long, the membranaceous portions unknown; puberulent; leaves with stout petioles, 5–6 mm. long, puberulent, attached at the base of the ocreae; blade orbicular to elliptic, 7×6 , 10×10 , 10.5×9 cm. long and broad, coriaceous, the apex rounded, the base rounded to slightly cordate, one basal lobe larger than the other, one or both slightly overlapping the petiole, the margin slightly revolute; midrib conspicuous on both surfaces, the veins 6 pairs, slightly conspicuous on both surfaces, the lower three close together; inflorescence terminal; immature, to 8 cm. long with a shorter basal branch, the rachis puberulent; flowers immature; fruit not known.

Dominican Republic. PROV. PUERTO PLATA: Puerto Plata, cliffs facing the sea at Arroyo Francés, *Ekman H-14402* (A, s).

Schmidt referred this collection to *Coccoloba verruculosa* with a question. In the general appearance of the leaves, this plant resembles *C. uvifera*. The similarity is accentuated by the nature of the leaf base and the branching habit of the inflorescence. The similarity to *C. costata* is found in the texture, the venation and the color of the leaf blades. Both *C. uvifera* and *C. costata* are found at Arroyo Francés and it is apparent that this single collection represents a hybrid of these two species.

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760; Hist. Stirp. Amer. 114, pl. 76. 1763.

Coccoloba cubensis Meisner, DC. Prodr. 14: 162. 1857.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. 13: 158. 1891, and all recent authors, not Jacquin.

Coccoloba longifolia Schmidt, Fedde Rep. Spec. Nov. 24: 73. 1927, not Fischer ex Lind.

Shrub or tree to 23 feet tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly swollen; ocreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; leaves of normal shoots with petioles 7–10 mm. long, glabrous, arising from the base of the ocreae; blades ovate, oval, oblong, elliptic, lanceolate or obovate, variable on one branch, 4×3.5 , 7×5.5 , 8×4.5 , 12×8 cm. long and broad, coriaceous, often shining above, dull beneath, glabrous, the apex rounded, obtuse, acute or acuminate, the base cuneate, rounded or subcordate, the margin entire; midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin; leaves of adventitious shoots on petioles 1–2.5 cm. long, with blades of varying shapes 17×8 , 24×13 , to 32×12.5 cm. long and wide; leaves of windswept specimens often much smaller than those of normal shoots with blades 2×1.3 to 3×2 cm. long and broad; inflorescence terminal 4.5–18 cm. long, rachis glabrous, the flowers on pedicels 2–4 mm. long, the staminate flowers 2–4 at each locus, the pistillate flowers borne singly at each locus, the bracts ovate, less than 0.5 mm. long, the ocreolae membranaceous, less than 0.5 mm. long, the hypanthium 1 mm. long, the perianth lobes ovate to oblong, 2–3 mm. long, 1–2 mm. broad, the functional stamens 1 mm. long, the sterile stamens rudimentary; fruiting pedicels 3–4.5 mm. long, the fruit globose to obpyriform, 10×7 , 12×8 , 13×8 mm. long and in diameter, the apex rounded, the perianth lobes imbricate and appressed.

COMMON NAMES: *Maivisse* (H), *raisin marron* (H), *resinier* (H), *uva cimarrona*, *uvero* (DR), *uvilla* (DR), *zamon maron* (H).

DISTRIBUTION: Florida, Bahamas, Greater and Lesser Antilles.

Dominican Republic. PROV. LA ALTAGRACIA: La Romana, *Taylor 384* (NY, US). PROV. AZUA: Azua, *Rose, Fitch & Russell 3934* (NY, US), *4415* (NY, US). PROV. BARAHONA: Beata Island, *Howard 12361* (GH), Palo Mino to Montasse near Polo, *Howard 12096* (GH), Barahona, *Fuertes 1104* (F, GH, MO, NY, S, US). PROV. BENEFACTOR: Río Arriba, *R.A. & E.S. Howard 8976* (GH). PROV. MONTE CRISTI: El Morro, *Howard 12536* (GH), *12538* (GH), *12531* (GH), *Moscoso 158* (SD); Santiago Rodríguez, Monción, *Valeur 254* (A, F, MICH, MO, NY, S, US). PROV. PUERTO PLATA: Sosúa, *Jiménez 1676* (GH); Savana de Guainamoca, *Eggers 2558* (B, NY, US). PROV. SAMANÁ: Lajana, *Abbott 1297* (US). PROV. SAN PEDRO DE MACORIS: San Pedro de Macoris, *Rose, Fitch & Russell 4444* (US). PROV. SANTIAGO: Angostura, *Jiménez 1824* (A). PROV. TRUJILLO: Jaina, *Faris 113* (US). DISTRICTO DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino 138* (G). San

Gabriel Island, *Miller* 1022 (US). Puerto Escondido, *Howard* 12139 (GH), 12145 (GH). LOCALITY UNCERTAIN OR NOT INDICATED: *Wright, Parry & Brummel* 477 (C, US); *Lopez, Eggers* 3387 (NY, US); Rio Verde, *Eggers* 2325 (M); *Sharff* 4 (F), 17a (F); *Jaeger* 313 (NY); *Sessé & Mociño* 5428 (F), 948 (F).

Haiti. DEPT. DU NORD OUEST: Tortue Island, La Vallée, *EC & GM Leonard* 11288 (MICH, GH, US); Mole St. Nicolas, *EC & GM Leonard* 13367 (US). DEPT. DU NORD: Bayeux near Port Margot, *Nash* 287 (F, NY). DEPT. DE L'ARTIBONITE: Ennery, *Leonard* 8909 (GH, NY, US), 9527 (US); Petit Rivière de l'Artibonite, *Picarda* 1580 (B); St. Michel de l'Atalaye, *Leonard* 7483 (MO, US), 7426 (US); La Brande to Mt. Blanche, *Nash & Taylor* 1649 (NY). DEPT. DU SUD: Ile Grande Cayemitte, *Eyerdam* 318 (F, GH, US); Navassa Island, *Rehder* 12 (A, NY, US), *Ekman* 10800 (S), *Proctor* 15478 (A, IJ); Jeremie, *Picarda* 1314 (B); Massif de l'Hotte, Trouin, *Ekman* 5944 (A, S); Miragoâne, *Prince Paul* 1313 (M). DEPT. DE L'OUEST: Goñave Island (Anse Galette), *Leonard* 3265 (B, NY, US), 3261 (US); Port au Paix, La Coup River, *EC & GM Leonard* 11138 (MO, NY, US); between Passe Aubert & Passe Chance aulme, *Ekman* 3819 (S, US); Jean Rabel, *EC & GM Leonard* 12704 (A, US); Fond Parisienne, *Holdridge* 1822 (GH, US); Morne Hospital, *Buch* 1839 (B); Petionville, *Picarda* 1410 (B).

This species is more common in Hispaniola than the few specimens cited above would indicate. In many areas *Coccoloba diversifolia* is in general use as a fence row tree, although I could never determine whether the plants were started as seeds or as cuttings.

The general misapplication of the names *Coccoloba diversifolia* and *C. laurifolia* by nearly all recent authors and their proper application has been discussed in an earlier paper (Jour. Arnold Arb. 30: 422-424. 1949).

Coccoloba fawcettii Schmidt, Fedde Rep. Spec. Nov. 24: 76. 1927.

Small tree (fide Ekman); branches tortuous, the nodes conspicuously swollen, the youngest parts densely golden-pubescent; ocreae 3-5 mm. long, membranaceous, pubescent, truncate or slightly bilobed at the apex; petioles 2-3 mm. long, pubescent, arising at the bases of the ocreae; blades cordate, 3.5×3 , 4×4 , 8×6 cm. long and broad, rigid and thin, papery in texture, the apex acute or obtuse, slightly apiculate, the base cordate, the margin entire, slightly undulate; midrib slightly prominent above, conspicuous below, primary veins 3-5 pairs, arcuate and anastomosing at the margin, scarcely impressed above, prominent beneath, the secondary venation prominent and reticulate below, the upper surface full and glabrous, the lower surface sparsely short pubescent; inflorescence terminal 1.8-3 cm. long, the rachis puberulent, the bracts triangular to 1.2 mm. long, spreading, the ocreolae membranaceous, to 1.2 mm. long, the pedicels shorter than the ocreolae; staminate flowers unknown, the pistillate flowers 1, rarely 2, at each locus, the hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5-2 mm. wide and 1.0-1.5 mm. long, the stamens rudimentary, less than 0.5 mm. long, the ovary ellipsoidal, 1.5 mm. long, sharply 3-angled; fruit not known.

DISTRIBUTION: Endemic to the Dominican Republic. Known only from the type collection.

Dominican Republic. PROV. BARAHONA: Mare-à-chat, Ekman H-6948 (B-type, s).

While the Berlin specimen of this collection has old inflorescences from which the flowers have fallen, the Stockholm specimen still retains a few open flowers. Schmidt states in the original description that the flowers and fruit are unknown. It is obvious that the Berlin specimen is the holotype. The staminate flowers and fruits are still unknown, but the pistillate flowers are described above.

The Berlin specimen consists of two fragments, one obviously from a mature shoot with inflorescences and the other from a more vigorously growing sterile shoot. The larger leaf size given in the description refers to leaves on the latter shoot. Truly adventitious shoots are not known.

In his original description Schmidt compared *Coccoloba fawcettii* with *C. pubescens* and *C. fuertesii*. It seems probable to me that *C. fawcettii* is a natural hybrid between these two species, both of which occur in the area where *C. fawcettii* was collected. Schmidt refers to the leaves of *C. pubescens* as being many times larger, yet some leaves of mature shoots in that species scarcely exceed those of the larger leaves on the type specimen of *C. fawcettii*. I was unable to find any plants of this species on a trip to the type location. Ekman stated in his field notes that the plant was "rare" and seen "only here." As a hybrid, *C. fawcettii* would derive the pubescence and reticulation from *C. pubescens* and the leaf shape and the swollen nodes from *C. fuertesii*.

Coccoloba flavescens Jacq. Hist. Stirp. Amer. 115. tab. 75. 1763.

Coccoloba pungens Urban, Symb. Antill. 5: 335. 1907; 8: 195. 1920.

Shrub, often with many trunks, to small tree with single trunk reaching 15 feet in height; bark gray, the youngest branches tan, slightly puberulent, geniculate, the nodes commonly swollen; ocreae membranaceous except at the base, to 3 mm. long, the base cartilaginous, ring-like, the petioles arising from this ring-like base, often appearing terminal due to geniculation of the stem; leaves of normal shoots with petioles 2–5 mm. long, puberulent to glabrous, the blades elliptic, ovate-elliptic or lanceolate-elliptic, 1.6×1.2 , 3.6×1.8 , 4.0×1.6 , to 5.6×2.2 cm. long and broad, rigid, flat or slightly umbonate, the apex acute, mucronate, the cartilaginous mucro to 1 mm. long, sharp and stiff, the base rounded to slightly cordate, the margin entire; venation not evident in fresh condition, only slightly evident when dry, the veins 10–20 pairs, equally developed; leaves of adventitious shoots similar in shape, 6.0×3.2 to 7.8×3.1 cm. long and wide; inflorescence terminal, 2–2.5 cm. long, the rachis glabrous, the bracts to 1 mm. long, slightly erose at the apex, the ocreolae less than 1 mm. long, the flowering pedicels short, those of the staminate flowers less than 1 mm. long, deciduous or rarely persisting and elongating slightly; staminate flowers borne singly at each locus, the hypanthium short, about 0.5 mm. long, the lobes 5 or 6, ovate, 2–3 mm. long, 1.5–2.5

mm. wide, the filaments 1–1.5 mm. long, the pistil rudiment to 2 mm. long; female flowers not seen; fruiting inflorescence stout, 1–4 cm. long, often strongly angled, the peduncles decurrent on the axis; fruit bright red, 4–5 mm. diameter, 6–9 mm. long, broadest at the middle, the apex rounded, the base slightly pedicellate, the perianth segments free to the middle, imbricate over the achene, strongly lined but the vascular bundles not evident.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Barahona, *Fuertes* 543 (F, GH, MO, NY, S, US); Las Salinas, *Howard* 12059 (GH), 12062 (GH). PROV. INDEPENDENCIA: Lake Enriquillo to Puerto Escondido, *Howard* 12132 (GH); Puerto Escondido to Rancho Viejo, *Howard* 12132 (GH).

Haiti. DEPT. DU NORD: Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4939* (S). DEPT. DE L'ARTIBONITE: Gonaïves to La Hotte Rochée, *Nash & Taylor* 1560 (NY). DEPT. DE L'OUEST: Fond Parisien, Étang Saumatre, *Leonard* 10138 (NY, US); Massif des Matheux, Croix des Bouquets, Morne à Cabrits, *Ekman H-989* (S, US). DEPT. UNCERTAIN: Cape Francois, *Ehrenberg s.n.* (B, NY); Poste Coudau, *Buch* 1024 (B-type of *C. pungens*).

This is a distinctive species apparently restricted to the dry areas at low elevation. Three leaf forms were seen in the field. The normal leaves were found on the much-branched and geniculate branches. Much smaller leaves were seen occasionally on fasciated lateral branches which are borne on wand-like shoots; see *Ekman H-3499*. Slightly larger than normal leaves are found on shoots of less compact habit, having longer internodes and these are considered to be adventitious shoots. All three habits and leaf sizes are commonly found on one plant. The leaves are rigid even when fresh and the short but sharp mucro is very much in evidence when collecting this species. The leaves when fresh have the characteristic grayish-green color dominant in arid regions of the West Indies.

The fruits of *C. flavescens* are distinctive in shape and in the nature of the perianth in fruit. The fine striations on the lobes of the fruiting perianth seem to be characteristic of this species. Much larger fruits are associated with *Ekman* 989. These appear to be teratological and gall-infested. The few fruits opened were devoid of seed.

Coccoloba fuertesii Urban, Symb. Antill. 7: 210. 1912.

Coccoloba taylori Urban, Fedde Rep. Spec. Nov. 13: 446. 1914; Symb. Antill. 8: 196. 1920; Ark. Bot. 20A(15): 29. 1926.

Coccoloba barkeri Ekman & Schmidt, Fedde Rep. Spec. Nov. 27: 104. 1929.

Tree to 40 feet; diameter at breast height ten inches, bark rough, in characteristic 1-inch squares; branches terete, the nodes swollen, glabrous or at most papillose; ocreae to 5 mm., membranaceous above, this part lobed to the base on one side, often flaring, thick and persistent below; leaves of normal shoots with petioles 2–6 mm. long, papillose, arising above the base; blades ovate to ovate-triangular, less frequently ovate-lanceolate,

elliptic or obovate, 2.5×2 , 4×3 , 5×4 , 5×5.2 , 6.5×4.5 to 7×3.7 cm. long and wide, generally broadest above the middle, coriaceous, entire, glabrous, the apex short- to long-acuminate, mucronate, the ultimate apex generally spine-tipped, the cartilaginous spine 0.5–2 mm. long, at times rounded to emarginate or almost bilobed through failure of the midrib to develop, the base cuneate to rounded, rarely acute or subtruncate, the margin entire; veins 5–10 pairs, subequal, prominently reticulate on both surfaces when dry, the veins arcuate, approaching but distinct from the cartilaginous margin of the leaf; leaves of adventitious shoots borne above the base of the ocreae 1–1.5 cm. long but occasionally to 3.4 cm. long, on petioles 1 cm. long, the blades broadly ovate to ovate-triangular to elliptic or ovate-lanceolate or elliptic-lanceolate, 8.2×6.2 to 16.5×9 cm. long and wide, often asymmetrical, the apex acute, acuminate, obtuse or rounded, the terminal spine present or absent, the base truncate, subtruncate or rounded; inflorescences equalling or surpassing the leaves, 2.5–6.5 cm. long, terminal, 1–4 at each locus; flowers sessile or on pedicels not exceeding 1 mm.; staminate flowers 1–4 at each locus, the pistillate flowers 1 at each locus, the bracts broadly ovate, 0.5 mm. long and wide, the ocreolae membranaceous, flaring, 0.5 mm. long; hypanthium to 1 mm. long, the perianth lobes oblong to ovate-orbicular, 1–1.3 mm. long and wide, the functional stamens to 1 mm. long, the sterile stamens with rudimentary anthers; functional pistil to 3 mm. long, the sterile pistil rudimentary; fruit red when mature, oblong or ovate, fleshy, 6–9 mm. long, 3–5 mm. in diameter, the hypanthium red in fruit, the perianth lobes coronate, 1–2 mm. long; fruit with a corky or woody sub-hemispherical sterile base, this often marked with a horizontal constriction and frequently attenuate below; achene brown or tan.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. DIST. DE SANTO DOMINGO: Santo Domingo on road to Puerto Plata, *Wright, Parry and Brummel 474* (GH, US). PROV. BARAHONA: Barahona, *Fuertes 716* (B-type), Palo Mino to Montasse on trail to Polo, *Howard 12065* (GH), Cañada Maluca, *Howard 12196* (GH). PROV. MONTE CRISTI: Restauración, *Ekman H-6250* (s). PROV. PUERTO PLATA: Sosúa at La Goleta, *Ekman H-14529* (s, US). PROV. SAMANÁ: Samaná, Pan de Azúcar, *Ekman H-15181* (s), Punta Arena, *Ekman H-14788* (s), Los Haitises near La Llanada, *Ekman H-15452* (s). PROV. TRUJILLO: Villa Altagracia, *Ekman H-11238* (A, s, US).

Haiti: DEPT. DU NORD OUEST: Massif du Nord, Port de Paix, Haut Piton, *Ekman H-4633* (B, s, US); Moustique Mts., Bassin Bleu, *E.C. & G.M. Leonard 14985* (US), *14986* (US), *15021* (A, GH, NY, US); Presqu'île du Nord, Port de Paix, Haut Moustique, *Ekman H-3639* (s); Jean Rabel, *E.C. & G.M. Leonard 13635* (A, GH, NY, US). DEPT. DU NORD: Massif du Nord, Morne Belance, *Ekman H-4911* (s); Massif du Nord, Bayeux, Morne Brigand, *Ekman H-2854* (s, US). DEPT. DE L'ARTIBONITE: Massif du Nord, Gros Morne, Morne Chabre, *Ekman H-5015* (s), Massif du Nord, Morne Bonpère, *Ekman H-4952* (A, s, US); La Brante to Morne Belance, *Taylor 1674* (B-type of *C. taylori*, NY); Ennery, *Ekman H-2468* (B). DEPT. DU SUD: Tiburon, Morne Sentier, *Ekman H-10597* (B, s, US); Morne Rochelois, Charlier, *Ekman H-9037* (A, s); Grand Cayemite,

Eyerdam 304 (A, F, GH, MO, NY, US), *Ekman* H-8927 (s, US), Miragoane, Petit-Rivière des Nippes, *Eyerdam* 398 (A, F, GH, NY, US). DEPT. DE L'OUEST: Massif de la Selle, Leogane near Citronniers, *Ekman* H-6464 (B-type of *C. barkeri*, s, US); Massif de la Hotte, Jacmel at Savanette, *Ekman* H-7081 (s, US).

The full variation in leaf size, shape and texture and the development of the terminal spine in this species must be seen in the field to be appreciated. One of my collections (*Howard* 12065) is represented by a series of twelve sheets taken from a single tree. This tree was 40 feet tall and 10 inches in diameter at breast height. Adventitious shoots developed in profusion from the trunk and from along the first main branch. The range of variation on the upper branches of the tree was significant, but this was exceeded by the variation on individual and different adventitious shoots. In general the leaves of the adventitious shoots were 2 to 3 times the size of the leaves on normal shoots. A second collection (*Howard* 12196) was made from a plant which consisted of a cluster of 14 trunks, the smallest less than an inch in diameter and the largest 8 inches and 20 feet tall. The original tree had been felled, but the stump remnant was still present. The smaller adventitious shoots produced the expected large leaves typical of such shoot systems, but the larger trunks retained only a few large leaves, while the majority were of the size range characteristic of the mature shoots. Other collections which show variations, apparently on single plants, are *Ekman* H-7081 and H-14788.

Urban recognized the affinity of *Coccoloba taylori* with *C. fuertesii*, but distinguished between them on the basis of petiole length and the shape of the leaves. The material which Urban studied consisted of a fast-growing, probably adventitious, shoot (the type of *C. fuertesii*), and two gnarled branches of a mature tree (the type of *C. taylori*). Comparable variation can be found very readily on one tree.

Coccoloba barkeri is based on a specimen of mature growth with inflorescences to 9 cm. long, these being 1-4 in number. Urban's distinction of *C. barkeri* from *C. taylori* on the basis of inflorescence length was made by comparing the longest inflorescence of the type specimen of *C. barkeri* with the average, if not the shortest, inflorescence of *C. taylori*. Recent collections demonstrate that *C. barkeri* is to be included with *C. taylori* in the species *C. fuertesii*.

Much of the material cited has been determined by others as *Coccoloba retusa* or *C. diversifolia*. *Coccoloba retusa*, a Cuban species, differs in having thinner textured leaves, less tumid nodes and more conspicuously pedicellate flowers and fruits. Leaves of *C. retusa* also lack the spiny tip found in *C. fuertesii*, but perhaps the most significant difference is the absence in *C. fuertesii* of the solid basal section of the fruits of *C. retusa*. The two species are very similar and perhaps eventually *C. fuertesii* should be considered a geographical variety of *C. retusa*. *Coccoloba diversifolia* of recent authors is now known as *C. swartzii* and is clearly distinct as to the shape of the fruit, the leaf venation and margin and the lack of any development of pedicels.

Coccoloba fuertesii is similar to *C. incrassata* and the relationship of these two species requires further study of the populations in the field.

***Coccoloba hotteana* Schmidt, Ark. Bot. 20A (15): 31. 1926.**

A shrub or depauperate tree to 5 feet tall; branches slender, terete, the nodes not enlarged; ocreae 5–6 mm. long, obliquely truncate at the apex, more or less bilobed, short ferruginous-pubescent; leaves of normal shoots with petioles 3–4 mm. long, ferruginous-short-pubescent, inserted at the base of the ocreae; blades elliptic, rarely ovate-elliptic or narrowly obovate, 3×1.8 , 4×2.5 , 4.5×2 cm. long and broad, thin coriaceous, the apex narrowed and generally abruptly acuminate and slightly apiculate, the base rounded or narrowed, the margin entire, slightly revolute; midrib lighter in color, slightly conspicuous above, prominent below, primary veins 4 or 5 pairs, evident on both surfaces, slightly arcuate to the margins then anastomosing parallel to the margin, the stomata depressed and appearing as punctations on both surfaces; leaves of adventitious shoots lanceolate-elliptic, rounded or narrowed at the base, acute at the apex or apiculate, to 8×3 cm. long and broad; inflorescence terminal 5–15 cm. long, glabrous to sparsely puberulent, the bracts ovate or triangular, to 0.5 mm. long, the ocreolae membranaceous, 0.5–1 mm. long, the pedicels about 1 mm. long; staminate flowers 1–4 per locus, the pistillate flowers borne singly at each locus, the hypanthium 1–1.5 mm. long, the perianth lobes ovate to suborbicular to 2 mm. long and wide, the fertile stamens 1.5–2 mm. long, the sterile stamens rudimentary, the sterile pistil rudimentary, the fertile pistil 1–1.5 mm. long; fruit subglobose, 6 mm. in diameter, the fruiting perianth lobes imbricate, the achene dark brown, smooth.

DISTRIBUTION: Endemic to Haiti.

Haiti. DEPT. DU SUD: Anse-à-Veau, *Ekman H-5399* (B-holotype, s, US); Ile Grande Cayemitte, *Ekman H-8954* (s), *Eyerdam 285* (A, F, GH, NY, US).

The type collection of this species represented by herbarium specimens from Berlin, Stockholm and the U.S. National Museum comprises nine plant fragments. Normally Erik Ekman collected material of good quality and a single specimen fills an herbarium sheet. It would be interesting to know what happened to this material. The nine specimens of plant material represent sterile mature growth, possible adventitious growth, staminate, flower-bearing branches, pistillate flower-bearing branches and fruiting twigs. One fruit is attached to an inflorescence which appears to be from a staminate plant. Additional fruits in the packet on this sheet are hollow and sterile. The type specimen from the Berlin herbarium consists of three fragments, one pistillate flowering axis, one fruiting axis and one sterile branchlet. In the packet on this sheet are three fruits on which both Schmidt and I have based our descriptions. If the fruit belongs with the specimen, its characteristics are of value in recognizing this species, but I question the authenticity of this fruit.

Coccoloba hotteana appears to be a distinct species. At the present it is known only from a coral reef west of Anse-à-Veau and from Ile Grande Cayemitte. Additional material is much desired. The species can be recognized by the shape and venation of the leaf, the apiculate apex to the leaves and the pubescence on the ocreae and inflorescence rachis.

Ekman did not approve of Schmidt's choice of name for this species, for La Hotte is a mountain range, while *C. hotteana* is known only from low coral reefs at sea level. He comments in the field notes of a second collection, "The specific name is misleading in a way. 'Hotteana' ought to be reserved for mountain plants."

***Coccoloba hotteana* Schmidt \times *C. uvifera* L., hybr. nov.**

Shrub (acc. to Ekman); branches terete, striate and canaliculate, puberulent to short pubescent; ocreae to 1 cm. long, strongly bilobed at the apex, puberulent, persistent; leaves of normal shoots with petioles 3–6 mm. long, stout, puberulent, arising from the bases of the ocreae; blades broadly elliptic to obovate-elliptic or orbicular, 6×4 to 7×6 cm. long and broad, coriaceous, the apex rounded to short apiculate, the base rounded, usually slightly asymmetrical, the margin flat; midrib conspicuous on both surfaces, the primary veins 5 or 6 pairs, conspicuous on both surfaces, the ultimate venation reticulate and conspicuous when dry, the upper surface glabrous, the lower surface puberulent and densely punctate-dotted with blocked stomata, the midrib and veins puberulent; leaves of adventitious shoots similar, to 10×8 cm. long and broad; inflorescence terminal, 10 to 25 cm. long, the rachis angular, puberulent, the bracts broadly ovate to 1 mm. long, the ocreolae 1 mm. long; pedicels 2–2.5 mm. long.

Haiti. DEPT. DU SUD: Ile Grande Cayemitte, northern coast in the Côtes de Fer, Ekman H-8950 (B, S), Eyerdam 303 (A, F, GH, MO, NY, US).

This hybrid is represented by collections of Ekman and Eyerdam numbered separately but made when these men were travelling together, on the same date and obviously from the same plant. This material in some respects resembles hybrids of *Coccoloba uvifera* and *C. costata* recognized from the vicinity of Puerto Plata and some specimens (e.g., Eggers 1762, the type of *C. verruculosa*) assigned to *C. costata* as a species. It seems distinct from these and appears to be derived from the parentage of *C. uvifera* and *C. hotteana*, both of which occur on Ile Grande Cayemitte. The leaf shape, particularly the nature of the leaf apex and the venation, appears to be derived from *C. hotteana*. The texture of the leaf, the nature of the inflorescence and the shape of the sterile fruits are those of *C. uvifera*. The inflorescences are old in the specimens cited above and a few fruits have been retained in packets. The flowering pedicels are borne, 3–5 at each node, on the inflorescence rachis, a character usually associated with staminate plants. As has been pointed out (Jour. Arnold Arb.

30: 390. 1949.), staminate plants of *Coccoloba uvifera* often form fruits which are of full size and normal shape but hollow or with aborted seeds or embryos. The fruits associated with the cited specimens resemble those of *C. uvifera*, not *C. hotteana*. They are obovoid, to 1.5 cm. long and 1 cm. in diameter. The fruits are strongly narrowed at the base and rounded at the apex with imbricated perianth lobes. The achene is dark brown and smooth but hollow or with a very small seed and is obviously infertile.

***Coccoloba incrassata* Urban, Symb. Antill. 7: 208. 1912.**

Coccoloba mansfeldii Schmidt, Ark. Bot. 20A(15): 29. 1926; Fedde Rep. Spec. Nov. 27: 103. 1929.

Shrub 10 feet tall to densely branched tree 20 feet tall; branches compact or geniculate, the lateral branches with short internodes often appearing as short shoots, the nodes conspicuously swollen, the branches often appearing moniliform, papillose to puberulent; ocreae membranaceous above, 1–2 mm. long, glabrous; leaves of normal shoots with petioles 1 mm. long, glabrous, inserted above the bases of the ocreae, the blades ovate-triangular, 1×0.7 , to 1.7×1.1 cm. long and wide, thick coriaceous, glabrous, the stomata and subsidiary cells clear, appearing as translucent dots, the apex attenuate to a spinose mucro, the spine about 1 mm. long, the base rounded to subtruncate; midrib cartilaginous, conspicuous on both surfaces, the veins anastomosing, conspicuous on both surfaces, 2 pairs of veins near the base of the blade separated from the upper pairs of veins, the veins reaching the margin without becoming arcuate, then fusing with the cartilaginous ring at the margin; leaves of adventitious shoots with petioles 4 mm. long, the blades lanceolate to lanceolate-ovate or elliptic-lanceolate 2.5×1.4 to 3×1 cm. long and wide, acuminate and pointed or narrowed to a rounded apex, base rounded to triangular, the adventitious stems densely pilose to completely glabrous; inflorescence terminal, shorter than the leaves or reduced to an almost sessile 1–4-flowered cluster; bracts and ocreolae minute, less than 0.5 mm. long, the pedicels approximately 1 mm. long; staminate flowers 1 or 2 per locus, occasionally 1–4 on adventitious flowering shoots, the pistillate flowers borne singly at each locus on the inflorescence; hypanthium to 1 mm. long, the perianth lobes 1 mm. long and 0.7 mm. wide, the fertile stamens to 1 mm. long, the fertile pistil 2 mm. long; fruit 5 mm. long and 3 mm. diameter, narrowed to a corky sterile base, coronate at the apex, on pedicels 1 mm. long.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. AZUA: Wright, Parry & Brummel 476 (GH, US). PROV. SAMANÁ: Los Haitises, La Marachita, Ekman 15531 (A, S, US).

Haiti. DEPT. DU NORD OUEST: Pendu, Buch 1269 (B-type, NY); Môle St. Nicolas, E.C. & G.M. Leonard 13356 (MO, US); Bombardopolis, E.C. & G.M. Leonard 13428 (A, GH, NY, US); Bombardopolis road south of Môle George, E.C. & G.M.

Leonard 13421 (MICH, US); Presqu'île du Nord Ouest, Môle St. Nicolas at Pap-à-foux, *Ekman* H-4487 (s, US); Presqu'île du Nord, Port de Paix, Haut Moustique, *Ekman* H-3648 (A, B, s, US). DEPT. DE L'ARTIBONITE: Ennery, *Leonard* 8861 (US); Massif du Nord, Ennery, *Ekman* H-2468 (s, US); Trois Rivières near Gros Morne, *E.C. & G.M. Leonard* 9893 (GH, MO, US); Mt. La Cidre, near St. Michel de l'Atalaye, *Leonard* 7397 (NY, US). DEPT. DE L'OUEST: Massif de la Selle, Anses à Pitres, *Ekman* H-6688 (s); Massif de la Selle, group Crete-à-Piquants, Port-au-Prince, Morne Aux-Fourques, *Ekman* H-5921 (B-type of *C. Mansfeldii*, s); Massif des Matheux, l'Arcahaie, *Ekman* H-9330 (B, s).

The presently accepted distinctions between *Coccoloba incrassata* and *C. fuertesii* are not entirely satisfactory. *Coccoloba incrassata* was based on a Buch collection from dry hillslopes at moderate elevation near Pendu. Urban compared the species with *C. armata* of Cuba which is clearly distinct in the manner of branching as well as in the shape and venation of the leaves. *Coccoloba mansfeldii*, described by Schmidt, was based on a sterile collection made by Ekman and is clearly a fast-growing shoot of *C. incrassata*. It is possible to assemble an almost complete series of specimens to show the transitions from the very small-leaved form typical of *C. incrassata* to the larger leaves of *C. fuertesii*. In almost every character selected, these two species tend to be closely associated. Nevertheless I am hesitant to merge the two without further field study of this complex. On a field label associated with his collection H-4911 which was assigned by Schmidt to *C. retusa*, Ekman writes, "evidently the same as n. ——— and n. ———. Resembles *C. retusa* Griseb. but is of course different, being in fact related with *C. incrassata* through a series of intermediate species." Few taxonomists split species finer than did Ekman and Schmidt; nevertheless it is interesting that Ekman felt he had seen and collected intermediate "species" between the two, although he never filled in the collecting numbers on his field label. For the present I distinguish *C. incrassata* on the basis of smaller leaves with fewer veins and with two pairs of these diverging near the base of the blade. The venation in specimens of *C. fuertesii* also differs from that of *C. incrassata*, in which the primary veins run straight to the margin before curving and fusing with the cartilaginous leaf margin. In *C. fuertesii* the veins divide or arch before reaching the margin, forming a network free from the cartilaginous margin. A parallel set of characters has been used to distinguish *C. retusa* and *C. northropiae* in Cuba and the Bahamas. Additional field study will be required to determine the value or validity of this distinction. The close association of *C. fuertesii* and *C. incrassata* is also indicated by the fruits, each possessing the sterile corky base to the achene. Only a few fruiting collections of *C. incrassata* are known, but in these the fruit appears to be smaller and the sterile base less differentiated than that of *C. fuertesii*.

Coccoloba krugii Lindau, Engl. Bot. Jahrb. 13: 145. 1890; Symb. Antill. 1: 222. 1899; Howard, Jour. Arnold Arb. 37: 337. 1956.

Coccoloba borgesensei Schmidt, Fedde Rep. Spec. Nov. 24: 75. 1927.

Coccoloba bõrgesenii forma *ovato-lanceolata* Schmidt, Fedde Rep. Spec. Nov. 24: 76. 1927.

Shrub or small tree to 19 feet tall; branches terete, glabrous, slightly geniculate and nodose; ocreae membranaceous; persistent, 3–5 mm. long; leaves of normal shoots with petioles 5–6 mm. long, corky at the base, arising from the bases of the ocreae; blades ovate to suborbicular, 2×1.8 , 4×3.5 , 5×4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the apex obtuse or rounded, the base cordate or rounded, the margin flat or recurved; midrib flat above, slightly prominent below, the primary veins 4–6 pairs, straight, bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above; leaves of adventitious shoots with petioles 1 cm. long, the blades cordate or elliptic to 7×6 cm. long and broad; inflorescence terminal 5–8 cm. long, the rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ocreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ocreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in cross section, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit.

DISTRIBUTION: The Bahamas, Hispaniola, Jamaica, Puerto Rico, Anagada, Antigua, Barbuda, St. Martin.

Dominican Republic. PROV. MONTE CRISTI: El Morro, *Ekman* 13143 (s), *R.A. & E.S. Howard* 12532 (GH), 12534 (GH), *Jiménez* 1356 (A).

Haiti. DEPT. DU NORD OUEST: Isle Tortue, Morne Barranca, *Ekman* 4314 (B-type of *C. bõrgesenii*, s, us); Port au Paix, Vallée des Trois Rivières, *Ekman* 3588 (B-type of *C. bõrgesenii* forma *ovato-lanceolata*, s, us); Port au Paix, *E.C. & G.M. Leonard* 15252 (A, GH, s, us).

Coccoloba krugii resembles *C. praecox* of Cuba and *C. buchii* of Hispaniola. It can be distinguished from these species by the angular rachis of the inflorescence and the angularity of the fruit.

Coccoloba bõrgesenii was described by Schmidt as having a puberulent rachis to the inflorescence. This "puberulence" appears to be a mixture of fungal hyphae, crystals of mercuric chloride and fibers of pressing material. *Coccoloba bõrgesenii* forma *ovato-lanceolata* is based on a specimen representing the adventitious shoots of this species.

Coccoloba krugii Lind. \times *Coccoloba uvifera* L.; Howard, Jour. Arnold Arb. 38: 216, 217. 1957.

Coccoloba scandens Ekman, Bull. Estac. Bot. Moca, Ser. B. 17: 14. 1927, nomen.

Shrub of 6 feet or small tree with habit of *Coccoloba uvifera*; young branches terete, striate, puberulent to pubescent; ocreae membranaceous,

oblique and slightly flaring at the apex, 1–1.5 cm. long, puberulent to pubescent; leaves of normal shoots on petioles 7–10 mm. long, the blades ovate to ovate-elliptic, 6×3 , 8×6 , 11×8 cm. long and broad, the apex obtuse to broadly rounded, rarely acuminate with an obtuse point, the base oblique, cordate to rounded, one basal lobe often overlapping the petiole; midrib and veins prominent below, sub-prominent above when dry, the ultimate venation reticulate, the primary veins 6 or 7, arcuate and anastomosing near the margin, 2 or 3 veins close to the base of the blade; leaves of adventitious shoots on petioles 7–10 mm. long, the blades ovate, ovate-elliptic or rarely ovate-lanceolate, 14×8 to 29×18 cm. long and broad; inflorescence simple, terminal, to 20 cm. long, the rachis slender, puberulent becoming glabrate; bracts broad, triangular-ovate, puberulent, the ocreolae membranaceous, to 1 mm. long, puberulent, the pedicels shorter than the ocreolae; staminate flowers 2–4 per locus, the pistillate flowers solitary at the nodes, the hypanthium to 1 mm. long, the perianth lobes orbicular, 1.5–2 mm. long and broad, the filaments of fertile stamens 2 mm. long; pedicels in fruit equalling to twice as long as the ocreolae, the fruit fusiform to fusiform-ovoid, 11 mm. long, 8 mm. in diameter, the perianth lobes not coronate.

DISTRIBUTION: Puerto Rico, Virgin Islands, Hispaniola.

Dominican Republic. PROV. MONTE CRISTI: Los Siete Hermanos, *Howard* 12524 (GH), 12525 (GH), 12526 (GH), 12527 (GH), 12528 (GH), 12529 (GH); *Ekman* H-13164 (s, US).

Haiti. DEPT. DU NORD OUEST: Tortue Island, La Vallée, *E.C. & G.M. Leonard* 15352 (US), 11320 (A, NY, US); Boucan-Guepes, *Ekman* H-9732 (s, US); Mare-Rocher, *Ekman* H-4122 (s, US); Môle St. Nicolas, *E.C. & G.M. Leonard* 13183 (MO, US), Port de Paix, *E.C. & G.M. Leonard* 11180 (NY, US), *Ekman* H-3935 (s).

This hybrid was recognized and described originally in relation to material from Puerto Rico and the Virgin Islands. Subsequent study of these troublesome populations and of the several series of collections cited above have shown additional and isolated occurrences of this hybrid in Hispaniola.

Ekman first discovered one population in 1925 on Ile de la Tortue and suggested in his field notes that it was a new species related to *Coccoloba uvifera*. A few days later he encountered it again along the sea coast west of Saline Michel near Port de Paix and indicated in his field notes that while sterile it was not the same as the Tortue plant and that it was "not *C. uvifera*, by no means." Schmidt annotated these specimens as *C. verruculosa* Lindau; Leonard, who collected in the same areas, also found the plant and used the same species identification. In 1929 Ekman visited Monte Grande in the Los Siete Hermanos island group off Monte Cristi and collected the plant there. In his field notes he identified the plant as *C. verruculosa* again, but comments, "I am beginning to feel suspicious about this. It is altogether too widely distributed and common to have escaped notice of the old collectors; e.g., Jacquin. How about

C. leoganensis?" In a brief published report of this last island trip Ekman refers to the occurrence of "*Coccoloba scandens*" on Monte Grande. *Coccoloba scandens* is published without description and, in any case, is a later homonym of *Coccoloba scandens* Benth., also a nomen nudum. The epithet "scandens" however was particularly appropriate, for several of the plants seen on Monte Grande had scrambling branches. As was true with populations of this hybrid in Puerto Rico and the Virgin Islands, there is a considerable range of variation between plants, accentuated in some cases by the normal variation between adventitious and juvenile shoots and those of more mature plants.

Coccoloba krugii, one of the suggested parents of this hybrid, is present on Tortue Island, Môle St. Nicolas and near Port de Paix where the hybrid has been collected. It was not found on any of Los Siete Hermanos, but occurs on El Morro near Monte Cristi. *Coccoloba uvifera* has been found in all locations where the hybrid occurs.

Coccoloba leoganensis Jacq. Enum. 19. 1760; Hist. Stirp. 113. pl. 178, f. 33. 1763; Pl. Amer. Pict. t. 60, f. 30, 1780.

Coccoloba rotundifolia Meisn. DC. Prodr. 14: 154. 1857..

Coccoloba uvifera var. *leoganensis* Willd. Sp. Pl. 2: 457. 1799.

Small tree to 20 feet tall, d.b.h. 6 inches; branches generally tortuous, striate, minutely pubescent, the nodes slightly swollen; ocreae 6 mm. long, membranaceous, minutely puberulent, obliquely truncate, light gray-green; leaves of normal shoots with petioles 7–15 mm. long, puberulent, swollen at the base, arising from the bases of the ocreae; blades orbicular, 3×3 , 5×6 , 7.5×8 to 9×9 cm. long and broad, subcoriaceous, glabrous above, glabrate below or with pubescence in axils of veins or along the midrib, the apex rounded, emarginate or obtusely short acuminate, the base shallowly cordate, the margin entire but generally slightly undulate; midrib and primary veins evident above and only slightly conspicuous below, the primary veins 5–7 pairs, the secondary venation evident but not conspicuous; fast-growing shoots not seen; adventitious shoots from trunk of tree slow-growing, tortuous and flattened, the leaf-bearing branches terete; leaves with petioles 2–3 mm. long, the blades similar in shape to those of normal branches 0.4×0.4 to 1.2×1.5 cm. long and broad; inflorescences terminal, 5–7 cm. long, the basal ocreae to 1 cm. long, the rachises puberulent, densely flowered, commonly thin to tenuous in flowering condition becoming thick in fruiting condition; staminate flowers 1–3 at each locus, the pistillate flowers generally borne singly at each locus, the bracts ovate, to 1.5 mm. long, the ocreolae 1–1.5 mm. long, membranaceous, puberulent; pedicels 1.5–2.0 mm. long, puberulent, articulated at the base and dehiscent after flowering, the flowers articulated, the hypanthium 1 mm. long, commonly narrowed to the pedicel, the perianth lobes broadly orbicular, 2–3 mm. long and broad, the functional stamens 1–1.5 mm. long, the fertile pistil 2.5 mm. long, the sterile stamens and

pistils abortive, to 0.5 mm. long; fruit ovoid, 4.5 mm. long, 3.5 mm. in diameter, narrowed at the base, the fruiting perianth red in color, the lobes tightly imbricate, longer than the hypanthium; achenes obtusely 3-angled, greenish brown.

LOCAL NAMES: *Uvero* (DR), *uvilla* (DR).

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino* 164 (GH). PROV. BARAHONA: Along the Rio Yaque, *Fuertes* 188 (BM, C, EDIN, F, GH, K, M, MO, NY, S, US). PROV. INDEPENDENCIA: Puerto Escondido, *Howard* 12185 (GH). PROV. LA VEGA: Cuesta de Piedra, *Eggers* 2376 (BM, GH, K, M, NY, US). PROV. LIBERTADOR: Between Restauración and Bánica, *Howard* 12555 (GH). PROV. MONTE CRISTI: Copey, *Howard* 12522 (GH); Villa Isabela, *Howard* 12521 (GH). PROV. SANTIAGO: Santiago to Quinigua, *Eggers* 2429 (A, B, C, US); Sabaneta, *Jiménez* 1737 (GH). PROV. TRUJILLO-VALDEZ: Bani, *Howard* 12045 (GH), 12048 (GH).

Haiti. DEPT. DU NORD OUEST: Port de Paix, Vallée des Trois-Rivières, *Ekman* H-3991 (s, US); Bassin Bleu, *E.C. & G.M. Leonard* 14603 (A, NY, US), 14782 (US); Cabaret, Baie des Moustiques, *E.C. & G.M. Leonard* 11820 (MICH, US), 12051 (A, GH, K, MO, NY, US); Jean Rabel, *E.C. & G.M. Leonard* 12071 (GH, US). DEPT. DE L'ARTIBONITE: Gonaives, *Buch* 654 (B); Gonaives to La Hotte Roche, *Nash & Taylor* 1586 (NY); Gonaives to La Branle, *Nash & Taylor* 1592 (NY, US). DEPT. DE L'OUEST: Between Port-au-Prince and Léogane, *Jacquin* s.n. (BM-holotype); Port-au-Prince, *Ekman* H-2110 (s); Montagnes du Trou d'Eau, Morne à Cabrits, *Ekman* H-990 (A, s, US); Ile de la Gonave, Pte. à Raquette, *Eyerdam* 54 (A, F, GH, MO, NY, US); Petit Gonave Island, *Leonard* 5233 (NY, US). DEPT. NOT KNOWN: Cape Francois, *Ehrenberg* s.n. (B, G-type of *C. rotundifolia*, NY).

Jacquin's descriptions of *Coccoloba leoganensis* are brief and the illustration cited above is of a single leaf which lacks any distinctive characteristics. All authors since Jacquin have referred *C. leoganensis* to the synonymy of *C. uvifera*. Willdenow established *C. leoganensis* as a variety of *C. uvifera* and Meisner accepted this placement, but with a query. Mr. Dandy, of the British Museum, kindly determined for me that the Jacquin specimen was there and verified the similarity to *C. rotundifolia*. I have since had the opportunity of seeing the material myself and it seems that at last the elusive name "*leoganensis*" can be properly placed. It certainly did not seem reasonable to me that Jacquin could not distinguish *C. uvifera* from other species.

The species *Coccoloba rotundifolia* Meisner was compared originally by the author with *C. leoganensis* and distinguished on the basis of smaller leaves. While Meisner did have a specimen from the smaller end of the range in size, his material can easily be matched with the more abundant specimens cited above.

Coccoloba leoganensis is a distinctive species both as living plants and as herbarium specimens. The habit of the plant, a low, densely

branched and rounded or flat-topped tree is striking. When in full flower the plants seen attract thousands of bees, so that collecting specimens becomes almost too competitive. In this species alone among those known from the Greater Antilles, the pedicels absciss immediately after flowering in the staminate inflorescences, and, if fertilization has not been effected, in the pistillate. A staminate inflorescence may have a few fully mature flowers at the apex and be naked and pitted below where flowers had been. This is particularly noticeable in fresh condition.

The fruits are described here for the first time. They are bright red in color and astringent, without any pleasant taste. The fruit is constricted at the base to a short stalk. The fleshy perianth lobes surround the achene tightly with only three lobes visible on the surface. The bracts and ocreolae enlarge slightly in fruit. This combination of characters would place the present species in the section *Campteria* of Lindau's classification. In total aspect the fruiting inflorescence resembles that of *Coccoloba nivea*, currently the only other West Indian species in this section.

Considerable individual variation in the amount of pubescence on the lower leaf surface was also noticed in living specimens in the field. The majority of mature leaves had a small amount of pubescence in the axils of the lateral veins on the lower leaf surface and additional pubescence along the midrib. On other plants the leaves were entirely glabrous below.

Perhaps the most unusual feature of *Coccoloba leoganensis* is the size of the leaves produced by lateral and adventitious shoots. Root sprouts and lateral stem sprouts were found on a number of trees near Bani in the Dominican Republic. This was the largest stand of *C. leoganensis* seen and here the species was the dominant tree in the dry thorn-shrub region at kilometer 80. The sprouts produced near the base of the trunk and on the trunk of these trees were short, compacted and contorted, in contrast to the normal elongate, fast-growing trunk sprouts of other species. In addition, the leaves are exceedingly small, ranging in size from 4×4 mm. to 12×15 mm. on petioles 2–3 mm. long. The leaves of these sprouts were generally orbicular and rounded at the apex, although some were ovate and obtuse at the apex. These sprouts all resembled *C. subcordata*. Careful attention was required to determine that these were parts of the plant of *C. leoganensis*. Even now, in dealing with the herbarium specimens, it has been necessary to recheck field notebooks to make certain that this point had been determined in the field and that the labels were not in error. Several of Leonard's collections (12071, 11820 and 14603) posed the same problem, although they had leaves grading to a larger size. In all of these collections, the petioles arise from the base of the ocreae, as in *C. leoganensis*, and not from the apex of the ocreae, as in *C. subcordata*. *Coccoloba subcordata* has an entirely distinct habit in the field and has short inflorescences, but in sterile herbarium specimens that two may well be confused. This is the only species of *Coccoloba* so far encountered in which the leaves of the sprout shoots are smaller instead of larger than the leaves of mature branches.

Coccoloba leonardii Howard, Jour. Arnold Arb. 30: 419. 1949.

Tree to 30 feet tall; branches terete, the nodes only slightly tumid, glabrous; ocreae subcoriaceous, the persistent part 3 mm. long, glabrous; leaves of normal shoots with petioles 8–11 mm. long, glabrous, arising about 0.5 mm. above the bases of the ocreae, the blade ovate, 6.5×4 , 8×5.5 to 11×7 cm. long and broad, coriaceous, the apex rounded to acute, the base rounded to slightly cordate, unequal, usually slightly decurrent on the petiole, the margin entire, flat; midrib not conspicuous above, the primary veins 5–7 pairs, ascending, arcuate, anastomosing near the margin, the ultimate venation reticulate, leaf surface glabrous, drying to a chestnut brown or ash color, the blocked stomata as seen on the lower surface brown in color; leaves of adventitious or fast-growing shoots elliptic, rounded or apiculate at the apex, often strongly cordate at the base, not larger than leaves of normal shoots in material seen; inflorescences terminal, 5.5–10 cm. long in fruit; staminate flowers 2–4 at each locus, the pistillate flowers solitary at each locus, the bracts 0.5 mm. long, the ocreolae about 1 mm. long, the pedicels short, less than 0.5 mm. long in fruit; hypanthium 0.5–1 mm. long, the perianth lobes 1.5 mm. long and broad, the fertile stamens 1 mm. long, the fertile pistil 2 mm. long, the sterile stamens and pistil rudimentary, less than 0.5 mm. long; fruit broadly fusiform, 10–11 mm. long, 5–7 mm. broad, the perianth lobes slightly coronate, these 1 mm. long, many-ribbed, drying black above and reddish brown below, the achene elongate, dark brown and shiny.

DISTRIBUTION: Haiti and Cuba.

Haiti. DEPT. DU NORD OUEST: Tortue Island, Basse Terre, *E.C. & G.M. Leonard 12466* (A-holotype, MO, NY, US), La Vallée, *E.C. & G.M. Leonard 11335* (MICH, US), *11381* (A, GH, K, US), *11421* (NY, US), *11423* (G, US); Pte. Petite Bois, *Ekman 4150* (s), Saline Michel near Port au Paix, *Ekman 3931* (s). DEPT. DU NORD: Morne la Vigie, Cap Haitien, *Ekman 2706* (s, US); Bayeux, *Nash 293* (F, NY). DEPT. DU SUD: Navassa Island, *Ekman 10843* (s, US).

Coccoloba microstachya Willd. Sp. Pl. 2: 459. 1800; Lindau, Engl. Bot. Jahrb. 13: 146. 1890; Howard, Jour. Arnold Arb. 37: 332. 1956, 38: 217. 1957.

Coccoloba klotzschiana Meisn. DC. Prodr. 14: 155. 1856.

Coccoloba obtusifolia Lindau, Symb. Antill. 1: 22. 1899, not Jacquin.

Shrub or tree to 20 feet tall; branches terete, the nodes tumid, pubescent or with hair primordia, the bark gray to tan in color; ocreae membranaceous, cylindrical, pubescent, 4 mm. long; leaves of normal shoots with petioles 3–6 mm. long, pubescent, arising from the bases of the ocreae; blades variable in size and shape, ovate, ovate-lanceolate, oblong or elliptic, 3.5×1.5 , 4×2 , 5.5×3.5 to 7×4 cm. long and broad, thin-coriaceous, usually turning black on drying, the apex acute, acuminate, rounded or emarginate, the base narrowed, rounded or slightly cordate,

the margin entire; midrib and vein evident but not conspicuous above, prominent below, primary veins 7–9 pairs, all glabrous above, pilose or glabrate below rarely persistently and densely pubescent; leaves of adventitious shoots on petioles to 7 mm. long with blades ovate-lanceolate to oblong, reaching 12×2.5 or 17×4 cm. long and broad, these generally more pubescent than leaves of mature shoots; inflorescence terminal, 5–10 cm. long, the rachis usually pubescent, tenuous, often geniculate, commonly recurved; staminate flowers 2 at each locus, the pistillate flowers solitary at each locus, the bracts broadly ovate, to 0.5 mm. long, puberulent, the ocreolae membranaceous, puberulent, to 0.5 mm. long, erect on the staminate plants, generally appressed or flattened on the pistillate, the pedicels shorter than the ocreolae or lacking, the hypanthium less than 1 mm. long, the perianth lobes 1–1.5 mm. long and 1 mm. wide; fruit sessile, generally ovate with distinctly coronate perianth lobes, to 6 mm. long and 4 mm. in diameter.

DISTRIBUTION: Dominican Republic, Puerto Rico, St. Thomas, St. Jan, Tortola, Virgin Gorda, Anguilla and St. Croix.

Dominican Republic. PROV. ALTAGRACIA: La Romana, *Ekman H-12098* (s, us). PROV. MONTE CRISTI: summit of El Morro, *Howard 12537* (GH). PROV. PUERTO PLATA: Puerto Plata, at La Boca, *Ekman H-14381* (A, s, us); Puerto Plata at Arroyo Francés, *Ekman H-14400* (s, us); between Puerto Plata and Maimon, *Eggers 2674* (B, M). PROV. SAMANÁ: Cabo Samaná, *Ekman H-14905* (s); Santa Barbara de Samaná, *Ekman H-15322* (B, s).

The variation in the size and shape of leaves and the amount of pubescence on plants of this species has been discussed in earlier papers in relation to *Coccoloba swartzii*. The few specimens from the Dominican Republic cited above represent nearly the extremes of variation. Most unusual is the shape of the leaves of adventitious shoots in several specimens. These are oblong—nearly linear-oblong—in shape. A similar variation also occurs in *C. costata* on the adventitious shoots of plants from the Samaná peninsula and from the eastern end of the island of Hispaniola.

Coccoloba nodosa Lindau, Engl. Bot. Jahrb. 13: 147. 1890.

Uvifera nodosa Ktze. Rev. Gen. 2: 561. 1891.

Small tree or bush 10–15 feet tall; branches of mature plant conspicuously nodose with short internodes, the branchlets often moniliform where leafless, sparsely short pubescent with golden to chestnut hairs; ocreae membranaceous, 3 mm. long, the apex acute, short pubescent; leaves of normal shoots with petioles 2 mm. long, puberulent, arising from the bases of the ocreae, the blades obreniform, orbicular or oblate, 0.5×0.9 , 1×2 to 2×2.5 cm. long and broad, coriaceous, generally drying black, sparsely short pubescent on both surfaces becoming glabrate, the apex broadly and shallowly emarginate or truncate, the base cuneate or rounded, the margin entire and flat, the blade flat; primary veins 3–5

pairs, mostly straight to the margin, then bifid and anastomosing, the venation evident above but slightly prominent below; adventitious shoots with nodes slightly swollen but not bead-like, the internodes striate, all densely ferruginous short-pilose, the ocreae 6–8 mm. long, deeply bilobed at the apex, membranaceous and deciduous above, chestnut-colored and pubescent, persistent below, this portion gray-green in color, the leaves with petioles 2–4 mm. long, densely gray pilose, arising from the bases of the ocreae, the blades cordate to ovate, to 6.5 cm. long and 5 cm. broad, the apex acute to obtuse, the base cordate to truncate, the margin undulate, the lateral branches of such shoots producing normal-sized leaves; inflorescence terminal 4–10 mm. long, puberulent to glabrous, the bracts triangular, membranaceous, to 1 mm. long, the ocreolae membranaceous, less than 1 mm. long; staminate flowers 1–3 at each locus, the pedicels 1 mm. long, the hypanthium 0.5 mm. long, the perianth lobes broadly ovate to orbicular, 1–1.5 mm. in diameter, the stamens 1–1.2 mm. long, the pistil rudimentary, less than 0.5 mm. long; pistillate flowers and fruit not known.

DISTRIBUTION: Endemic to the Dominican Republic.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: Llano Costero, El Manielito, *Ekman H-11289* (A, s, us); Llanura de Santo Domingo at Las Rosas, *Ekman H-5804* (s); La Yuca, *Jiménez 3401* (A); on road from Santo Domingo City (Ciudad Trujillo) to Puerto Plata, *Wright, Parry and Brummel 475* (GH, NY, us). Without specific location: *Bertero 928* (B-type, M), *R. Schomburgk 65* (B).

Until recently I had considered the sterile collection *Ekman 5809* to represent the adventitious shoot condition of this species. Several months ago Dr. José Jiménez of the Dominican Republic sent for identification a small specimen of *Coccoloba* which I assigned to this species. Since I had not been able to locate plants of this species during several visits to the Dominican Republic, I asked Dr. Jiménez to obtain additional material to show all possible leaf variation in this plant. Such specimens were collected for me by Professor Marcano of the Instituto Botanico "Rafael M. Moscoso" and were forwarded by Dr. Jiménez. I am indebted to both gentlemen for the material essential to a better understanding of leaf variation in *Coccoloba nodosa*. Unfortunately, the plants under observation have not flowered and hence several details of the description remain uncompleted.

Coccoloba nodosa may eventually include *C. picardae*. When Urban described the latter species he distinguished between them on the basis of the swollen nodes and obtriangular leaves of *C. nodosa*. He also noted that the flowers are in multiples in *C. nodosa*. This aggregation of flowers or pedicels is usually found in the staminate flowers, while the pistillate flowers are borne singly at each locus on the rachis. On the basis of normal shoots the leaves of *C. nodosa* and *C. picardae* are similar; however, until pistillate flowers and fruits are obtained for *C. nodosa* and adventitious shoots for *C. picardae*, the species should be kept distinct. *Coccoloba*

nodosa has been collected at lower elevations while *C. picardae* has been found only at elevations above 5000 feet.

***Coccoloba pauciflora* Urban, Symb. Antill. 7: 209. 1912.**

Coccoloba neurophylla Urban, Fedde Rep. Spec. Nov. 19: 1. 1923; Ark. Bot. 20A(15): 30. 1926.

Coccoloba mornicola Urban, Fedde Rep. Spec. Nov. 13: 446. 1914; Ark. Bot. 20A(15): 30. 1926.

Coccoloba fulgens Leonard, Jour. Wash. Acad. Sci. 17: 66. 1927.

Coccoloba nalgensis Schmidt, Fedde Rep. Spec. Nov. 32: 80. 1933.

Shrub or tree to 28 feet tall; branches terete, the nodes not swollen, short ferruginous pubescent, almost pilose or becoming glabrous, the hair bases and the often resinous stomatal excretions frequently resembling peltate scales; ocreae membranaceous, 3–8 mm. long on normal shoots, oblique at the apex, ferruginous pubescent; leaves of normal shoots with petioles 2–10 mm. long, generally pilose at least on the adaxial surface, arising at the bases of the ocreae, the blades obovate to obovate-elliptic, 1.5×0.8 , 2×1.4 , 3×1.5 , 4×2 to 5×3 cm. long and wide, subcoriaceous, glabrous or with conspicuous or inconspicuous stomatal excretions, the apex rounded to shortly and abruptly acuminate, occasionally truncate, often asymmetrical, the base cuneate; primary veins 3–5 pairs, prominent on both surfaces when dry; adventitious shoots terete, the ocreae to 1.5 cm. long, conspicuously ferruginous pilose or puberulent, the leaves with petioles 1.3–1.7 cm. long, the blades ovate-elliptic to ovate-lanceolate and 17×9 or 14.5×8 cm. long and broad, these broadly cuneate to acute at the base, broadest below the middle and acuminate at the apex, or blades obovate to obovate-lanceolate to 14×7 cm. long and wide, these broadest above the middle, cuneate at the base and acute at the apex; inflorescences terminal on axillary shoots of varying lengths and ages, the youngest often appearing as axillary clusters of flowers, the axis 2–3 rarely 4 cm. long, densely ferruginous pilose or puberulent at the base or, when young, soon becoming glabrate, the bracts broadly triangular, puberulent, the ocreolae 0.5–0.75, rarely 1 mm. long, tubular and not spreading; pedicels 1 mm. long in flower, those bearing staminate flowers increasing to 2 mm. long before or after abscission of flowers; staminate flowers in clusters of 2–3, the pistillate flowers borne singly at each locus; hypanthium 0.5–0.75 mm. long, the perianth lobes orbicular, 1–1.5 mm. long and broad, the functional stamens 1.2–1.4 mm. long, the sterile stamens less than 1 mm. long, the functional pistil 2 mm. long, the abortive pistils less than 0.5 mm. long; fruit brilliant to dull red when fresh, reddish brown when dry, ovoid to pyriform 6–7 mm. long, 4–5 mm. in diameter, slightly coronate at the apex, the fruiting hypanthium extending above the middle, the lobes of the perianth imbricate and covering the achene at the apex; achene chestnut-brown.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: El Aguacate to crest on road to

Pedernales, *Howard* 12572 (GH), 12586 (GH); La Tierra Fria, *Howard* 12210 (A); Polo, *Howard* 12239 (GH). PROV. LA VEGA: Constanza, *Türckheim* 2955 (B-lectotype, M, NY). PROV. SAMANÁ: Samaná, Laguna, Los Bañaderos Prietos, *Ekman* H-15135 (s, US). PROV. SAN RAFAEL: Loma Nalga de Maco, *Ekman* H-6322 (B-holotype of *C. nalgensis*, s, US). PROV. SANTIAGO RODRIGUEZ: Monción, *Ekman* H-12085 (B, s, US).

Haiti. DEPT. DU NORD OUEST: Massif du Nord, Port de Paix, Haut Piton, *Ekman* H-3697 (B, s, US); Bassin Bleu, Morne Haut Piton, *E.C. & G.M. Leonard* 15043 (A, GH, US), 15046 (MO, NY, US), 15064 (US). DEPT. DU NORD: Massif du Nord, Bayeux, Morne Brigand, *Ekman* H-2853 (s, US). DEPT. DE L'ARTIBONITE: Ennery, Puilboreau Pass, *Leonard* 9145 (B, GH, NY, US-type of *C. fulgens*); Massif du Nord, Gros Morne, Morne Belance, *Buch* 811 (B-type of *C. mornicola*), *Ekman* H-4910 (s). DEPT. DU SUD: Massif de la Hotte, Nouvelle Touraine, *Ekman* H-1657 (A, s). DEPT. DE L'OUEST: Massif de la Selle, Morne Tranchant near Godet, *Ekman* H-1953 (s); Massif de la Selle, Petionville, *Ekman* H-1657 (US); Massif des Matheux, Grand-Bois, Cornillon, *Ekman* H-5686 (s, US); Massif de la Hotte, Petit Goave, road to Morne Calumette, *Ekman* H-7304 (s); Fond Verettes, *Leonard* 5347 (B-type of *C. neurophylla*, US).

To the present, *Coccoloba pauciflora* has been represented only by the original collection of Türckheim; *Coccoloba nalgensis*, also, is known from the type collection alone and the several collections cited above, assigned indiscriminately to either *C. mornicola* or *C. neurophylla*. Both *Coccoloba mornicola* and *Coccoloba neurophylla* were described on sterile material and in each case Urban published a note adding to the description when additional material became known. Unfortunately, the additional material has been staminate in the case of *C. mornicola* and pistillate in the case of *C. neurophylla*. Here again arises the necessity of combining names and species based on the erroneous idea that the flowers are perfect. The study of a considerable number of plants and populations of this species in the Dominican Republic has allowed me to describe the range of variation found in the leaves, pubescence and inflorescence of this species.

Coccoloba pauciflora was so named for the short inflorescence axis and the few flowers produced. The nature of the leaf margin was also a characteristic which Urban used in describing the plant. It is possible to find short inflorescences at the top of many plants where the inflorescences terminate axillary branches. At a lower level in the tree, however, the lateral branches, which are little more than short shoots, have elongated slightly and the inflorescence produced is longer.

Leaf variation is considerable, both within a population and on the same plant, as to size, texture and apex. The shape of the leaf apex is related either to the development of the midrib or to its failure to develop at the apex. Three conditions are found on different plants, or on the same tree on one branch, or on different branches: (1) the midrib can be uniformly developed to the apex, in which case the tip of the blade is acuminate; (2) the midrib may apparently fail to develop at the apex of the blade, in which case this area is vascularized by the upper pair of primary veins; or (3) a remnant of the midrib may be present or absent. In this situation the apex of the leaf is obtuse or rounded.

In the third condition observed, the midrib fails to develop to the tip of the blade and one of the upper pair of primary veins dominates the other. In this case the leaf apex is asymmetrical. Examples of the three types of leaf apices on one plant are found in the collections of *Ekman H-2853*, *H-1657* and *Howard 12586*, the latter collected especially for this purpose.

The smaller range of leaf variation in this species is represented by the specimen *Ekman H-6322* which Schmidt selected as the type of his *Coccoloba nalgensis*. The herbarium sheets of this collection bear an unpublished specific name based on the province of Azua where, it is said, this collection was made. Loma Nalgo de Maco, as now known, is in San Rafael Province. While Schmidt describes the leaves as 1–2 cm. long and 0.8–1.2 cm. wide, the majority of the leaves on the three examples of this number are at the smaller end of the range given. Several more recent collections (e.g., *Ekman H-12805* and *Howard 12572*) are intermediate between the type collection of *C. nalgensis* and the majority of the specimens cited above. One collection (*Howard 12572*) consists of several specimens from a single tree made to show a full range of variation from the smallest leaf and shortest inflorescence to the larger ones more typical of the expanded species concept here employed. Unfortunately, this single tree did not have any adventitious shoots. Plants of this series approach *C. picardae* in form and it is possible that additional collections will demonstrate that *C. picardae* should be included in this species, in which case *C. picardae*, the earlier name, must be used.

Several excellent examples of plants with well developed adventitious shoots were found in the mountains around Barahona. One of these (*Howard 12239*) was a 25-foot tree in full flower. Several of the lateral branches possessed side shoots with normal leaf size and shape (obovate with a rounded apex 3 cm. long and 1.5 cm. wide), while the apex of the branch had longer internodes and larger leaves, some of these reaching a length of 10 cm. and a width of 4 cm. Strict adventitious shoots arising from the base of this tree were wand-like with long internodes and obovate leaves 14 cm. long and 7 cm. wide above the middle. A second plant in the same general area was growing on a steep hillside and at an angle. The tree was sterile but the apex of the plant had branches with obovate leaves averaging 3.7 cm. long and 1.7 cm. wide with acute to acuminate apices. From the trunk of this plant were developed numerous adventitious shoots, these all arising vertically and at an angle to the tree. The leaves on these adventitious shoots were ovate-elliptic to ovate-lanceolate and broadest at or slightly below the middle. The leaves ranged to 17 cm. long and 9 cm. wide. They were broadly cuneate to acute at the base and acuminate at the apex. The contrast between the normal foliage and that of the adventitious shoots was startling when seen in the field and was almost unbelievable when the herbarium specimens were studied in the laboratory.

An *Ekman* collection from the Samaná peninsula is referred here. Although it is sterile and represents an adventitious shoot, it matches the

material of *Howard 12239*. Schmidt studied this collection and referred to it as "*C. subtruncata* forma." Neither *C. pauciflora* nor "*C. subtruncata*" have been reported from the Samaná peninsula.

***Coccoloba picardae* Urban, Symb. Antill. 5: 336. 1907.**

Shrub to tree of 30 feet; branches terete, the nodes not swollen, short ferruginous-pubescent becoming glabrous, the branchlets often arranged in one plane; ocreae short, 1–2 mm. long, ferruginous-pubescent; leaves of normal shoots with petioles 1.5–2 mm. long, almost villose pubescent on the adaxial side, arising from the bases of the ocreae; blades orbicular to obtriangular, 1.1×1.2 , 1.6×1.2 , 1.7×1.7 to 2.5×2.5 cm. long and broad, coriaceous, stiff and rigid even when fresh, stomatal excretions evident on the lower surface, the apex rounded, subtruncate to submarginate, often asymmetrical, the base rounded, to subtruncate or narrowed and nearly cuneate, the primary veins 3–4 pairs, the venation reticulate and conspicuous on both surfaces when dry; adventitious shoots or leaves not known; inflorescences terminal on lateral short branches, often appearing capitate, the rachis 2–5 mm. long, the bracts broadly triangular 0.5–1 mm. long, the ocreolae to 1 mm. long, the pedicels 0.5–1.4 mm. long; staminate flowers 1–2 per locus, the pistillate flowers 1 at each locus, the hypanthium to 0.5 mm. long, the perianth lobes suborbicular 1.2–1.4 mm. long and broad, the fertile stamens 1–1.5 mm. long, the sterile stamens 0.5 mm. long, the functional pistil 1.5 mm. long, the pistillate rudiment less than 0.5 mm. long; fruit ovoid, 3–4 mm. long, 2–3 mm. broad, the hypanthium shorter than the lobes in fruit, the achene not coronate.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Crest of ridge between El Aguacate and Pedernales, *Howard 12594* (GH).

Haiti. DEPT. DE L'OUEST: Massif de la Selle, Petionville on top of Morne Tranchant, *Ekman H-1163* (S, US), *Picarda 784* (B-holotype), *Buch 1614* (B), *1663* (B), *Leonard 4385* (GH, NY, US); Guimbi Galata, Morne des Commissaires, *Holdridge 1280* (GH, NY, US).

This species is very similar to the small-leaved variation of *Coccoloba pauciflora* and may eventually prove to be part of the same complex. For the present, the two species can be distinguished on the basis of the very short inflorescences, the leaves broader than long, the non-coronate fruit and the single-plane branching of *C. picardae*.

***Coccoloba pubescens* L. Syst. Nat. ed. 10. 1007. 1759; Hooker, Bot. Mag. t. 3166. 1832; Fawcett & Rendle, Jour. Bot. 51: 123. 1913; Howard, Jour. Arnold Arb. 38: 227. 1957.**

Scortea arbor Americana, amplissimis foliis, aversaparte nervis extantibus hirsutie ferruginea refertis; Plukenet, Phytographia t. 222, f. 8. 1691.

Coccoloba rubescens L. Sp. Pl. ed. 2. 523. 1762.

Coccoloba grandifolia Jacq. Enum. 19. 1760.

Coccolobis pubescens Sandwith, Jour. Bot. 78: 98. 1940.

Coccolobis antiguensis Sandwith, Jour. Bot. 78: 98. 1940.

Mature tree to 40 feet tall, d.b.h. 12 inches, much branched above a well defined trunk; branches terete, swollen at the nodes, the lenticels not conspicuous, tomentose to pilose; the ocreae to 1 cm. long, generally completely deciduous, pubescent; leaves of completely mature plants varying considerably in size and shape, the petioles 3–6 mm. long, inserted below the ocreae, densely short pubescent, the blades broadly orbicular to orbicular-ovate, 4×6 , 7.5×10 cm. long and broad, grading into size of leaves of adventitious shoots, rugose or bullate, the apex rounded, the base cordate, the basal lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely to sparsely pubescent below or glabrate, the margin undulate, the venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; adventitious shoots generally strict and sparsely branched, to 30 feet tall, the branches stout, terete, slightly swollen at nodes, strongly grooved or striate, the ocreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below, the petioles stout 1–2 cm. long, densely tawny pubescent, the blades large, generally orbicular except for the terminal leaf, frequently broader than long, 30×40 , 50×80 cm. long and broad, coriaceous, rugose or bullate when mature, thin and plane when young, the apex rounded, the base rounded to cordate, the basal lobes commonly encircling the stem, the terminal leaf commonly rhombic, longer than broad when mature, densely tomentose, the veins slightly impressed above, all venation conspicuous and reticulate below, the midrib and secondary veins persistent-pubescent above, the others sparsely pubescent when young, becoming glabrate above, the veins and leaf surface pubescent or becoming glabrate below, the margin irregular, commonly undulate; inflorescences terminal, often stout, the basal ocreae to 7 mm. long, membranaceous, the peduncle to 1.5 cm. long, the rachis minutely and often densely puberulent, 10–18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, the bracts broadly ovate, about 1 mm. long, puberulent, the ocreolae membranaceous, spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2–4 per locus, the pistillate flowers 1–3 per locus, the pedicels 2–3 mm. long, the hypanthium 0.5–1 mm. long, the perianth lobes broadly orbicular, 1.5 mm. long, 2 mm. wide, puberulent, the fertile stamens 2.5 mm. long, the sterile stamens rudimentary, 0.5–1 mm. long, the fertile pistil glabrous or rarely slightly puberulent on the ovary, the sterile pistils glabrous, rudimentary, 0.5–1.5 mm. long; fruit globose to ovoid, 5–6 mm. long and 4–5 mm. in diameter, the fruiting perianth imbricate at the apex, not coronate, the fruiting hypanthium with conspicuous vascular bundles; achene sub-globose, dark brown, shining, slightly triradiate at the apex, the fruiting pedicels puberulent, 3–4 mm. long.

LOCAL NAME: *Gamelle* (H), *Hojancha* (DR).

DISTRIBUTION: Hispaniola, Puerto Rico, Barbuda, Antigua, Montserrat, Nevis, Guadeloupe, Dominica, Martinique, St. Lucia.

Dominican Republic. DIST. DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino* 137 (GH); Cuenca, *R.A. & E.S. Howard* 9884 (A). PROV. BARAHONA: El Caiman, between Enriqueillo and El Can, *Howard* 12187 (GH); Beata Island, *Howard* 12352 (GH); Mare-à-Chat, *Ekman* H-6947 (S, US). PROV. ESPAILLAT: Moca, *Eggers* 2559 (B, GH, M, NY, US). PROV. INDEPENDENCIA: Between Puerto Escondido and Rancho Viejo, *Howard* 12143 (GH). PROV. LIBERTADOR: Between Restauración and Bánica, *Howard* 12569 (GH). PROV. PUERTO PLATA: Hoja Anchas, *Jiménez* 2088 (A). PROV. SAMANÁ: Pilón de Azúcar, *Abbott* 401 (US). LOCALITY UNCERTAIN: *Prince Paul* s.n. (M).

Haiti. DEPT. DU NORD QUEST: Bassin Bleu, *E.C. & G.M. Leonard* 15199 (A, US); Môle St. Nicolas, *Ekman* H-4489 (S). DEPT. DU NORD: Between Pignon and Hinche, *Holdridge* 1272 (GH, US); Ranquitte, *Christ* 2090 (B). DEPT. DE L'ARTIBONITE: St. Michel de l'Atalaye, *Leonard* 7296 (NY, US); Hinche, *Ekman* H-6142 (A, S, US). DEPT. DU SUD: Massif de la Hotte, Morne Rochelois, Charlier, *Ekman* H-9035 (B, S), H-9086 (S); Miragoane, *Eyerdam* 396 (GH, NY, US); Port-à-Piment, *Ekman* H-336 (S); Camp Perrin, *Ekman* H-249 (S). DEPT. DE L'QUEST: Petit Gonave Island, *Leonard* 5242 (S); montagnes du Trou d'Eau, Fond-des-Oranges, *Ekman* H-2312 (S).

The variation in leaf shape and size in specimens of *Coccoloba pubescens* encountered in the herbarium and as seen in the field has been discussed in a previous paper (Howard, Jour. Arnold Arb. 38: 229-231. 1957). These variations contrast the adventitious and juvenile shoot systems from those of mature trees. A greater proportion of the specimens cited above represents mature plants than would a comparable number of specimens from other islands. A similar observation was made in the field; i.e., the number of individuals of this species represented by mature plants was greater in Hispaniola than on other islands where the species seemed almost typified by the adventitious shoot condition of very large leaves. In most of Haiti and western Dominican Republic the plants of *Coccoloba pubescens* grew relatively unmolested. In eastern Hispaniola and on the other islands of the Antilles, mature or undisturbed specimens were rarely encountered and second-growth habit seemed most abundant. A population of this species near Cuenca was visited first in 1946 and at two five-year intervals since, but the plants, though larger and with some now in flower, retain the characteristic adventitious leaves.

One known hybrid of *Coccoloba pubescens* with *C. uvifera* is described in this paper and I have suggested the possible hybrid condition and origin of *C. jawcettii* and *C. ceibensis*, with *C. pubescens* as one of the parents of each.

Coccoloba samanensis Schmidt, Fedde Rep. Spec. Nov. 32: 81. 1933.

Small to medium-sized tree (fide Ekman); branches terete, lightly striate, puberulent, the nodes slightly swollen; ocreae 6-10 mm. long,

membranaceous glistening, puberulent to glabrous; leaves of normal shoots with petioles 6–8 mm. long, puberulent with shining hairs, 6–8 mm. long, inserted at the bases of the ocreae; blades ovate to elliptic, rarely orbicular-ovate, 5×4 , 7.5×5 to 7.5×8 cm. long and broad, coriaceous, apex obtuse, short and abruptly acuminate or rarely subtruncate, the base obtuse to slightly cordate, the margin entire, slightly revolute, the midrib impressed above, prominent below; the primary veins 6 or 7 pairs, inconspicuous above, prominent below, the ultimate venation minutely reticulate; leaves of adventitious shoots with petioles 1.4 cm. long, similar to those of normal shoots in shape, to 12×10 cm. long and broad; inflorescences terminal, 8–18 cm. long, the rachis glabrous, lightly puberulent to short pilose, the bracts broadly ovate, to 1 mm. long, the ocreolae membranaceous, flaring, 2- or 3-lobed, to 1 mm. long, puberulent; staminate flowers not known, the pistillate flowers on pedicels shorter than the ocreolae, the hypanthium 0.5 mm. long, the perianth lobes obovate to elliptic, 1.2 mm. long, puberulent, the stamens abortive, about 0.5 mm. long, the ovary to 1.5 mm. long; fruit ovate with conspicuous coronate perianth lobes, 3 mm. long and 3 mm in diameter, the vascular bundles conspicuously developed, the achene globular, smooth, tan in color.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. SAMANÁ: Los Haitises, Boca del Infierno, *Ekman H-15392* (s); Samaná, slopes of Pan de Azúcar, *Ekman H-15175* (A, B-type, s, us), *H-15095* (s); Samaná, Laguna, Los Bañaderos Prietos, *Ekman H-15125* (s).

This species is poorly known and is represented in large part by sterile material. The collection *Ekman H-15392* has a very few fruits in a packet and two other specimens possess a few flowers. In general appearance this species is similar to *Coccoloba costata*, although in the details of smaller fruits, the coronate perianth lobes and the sessile flowers, it is distinct from *C. costata*, as well as from other species of Hispaniola. This is one of the few species of *Coccoloba* with the leaves shiny on the upper surfaces when dry. The coloration of the vein pattern is conspicuous when dry, giving the impression of a minute network or reticulum.

Coccoloba subcordata (DC.) Lindau, Engl. Bot. Jahrb. 13: 131. 1890; Symb. Antill. 7: 209. 1912.

Erythroxylon subcordatum DC. Prodr. 1: 575. 1824.

Low shrub to 6 feet tall with numerous arching branches, these branching in one plane, the short-shoots conspicuously developed, the branchlets terete, ferruginous pubescent, the nodes not enlarged; ocreae 2–5 mm. long, membranaceous, of uniform texture, obliquely truncate to slightly bilobed at the apex, appressed, minutely puberulent; leaves of normal shoots with petioles 1.5–2.5 mm. long, puberulent, arising from the upper portion of the ocreae, the blades broadly suborbicular to ovate, 2×2 , 4×4 , 11×10 mm. long and broad, subcoriaceous, glabrous

above, glabrate below, rarely puberulent on the veins, commonly shining on both surfaces and slightly paler in color below, the apex rounded to emarginate, the base rounded to rounded-cordate, the margin entire, often slightly undulate, primary veins 3–5 pairs, occasionally clustered near the base, the veins forking and anastomosing near the margin, reticulate, only slightly prominent on both surfaces when dry; inflorescences terminal on lateral branches or short-shoots, 4–10 mm. long, the rachis puberulent or glabrate, the bracts short triangular to 0.5 mm. long, the ocreolae membranaceous, flaring at the apex, to 1 mm. long; pedicels solitary or rarely 2 in the axil of each bract, to 2 mm. long at maturity, the hypanthium tapering from the apex of the pedicel, about 0.5 mm. long, the lobes ovate, about 1 mm. long and broad; fertile stamens 1–1.5 mm. long, the filaments slightly united at the base, the sterile stamens aborted or rudimentary, less than 0.5 mm. long, the functional ovary strongly 3-angled; fruit broadly ovoid, broadest below the middle, 4 mm. long, 3–3.5 mm. in diameter, the fleshy perianth bright red, the perianth lobes $\frac{1}{2}$ – $\frac{2}{3}$ the length of the fruit, strongly imbricated, the achene pale tan in color.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Las Salinas, *Fuertes 822* (F, GH, US), *Howard 12060* (GH); Beata Island, *Howard 12488* (GH). PROV. BENEFACCTOR: San Juan, Loma de Jayaco, *Ekman H-13471* (S, US). PROV. INDEPENDENCIA: Between Lake Enriquillo and Puerto Escondido, *Howard 12130* (G). PROV. NOT KNOWN: *Bertero s.n.* (B, G-type of *Erythroxylon subcordatum*, GH-photos, M).

Haiti. DEPT. DU NORD OUEST: Jean Rabel, *E.C. & G.M. Leonard 12761* (A, GH, NY, US); Presqu'île du Nord-Ouest, Baie de Henne, *Ekman H-4536* (S, US). DEPT. DE L'ARTIBONITE: Gonaïves, *Leonard 10058* (GH, NY, US). DEPT. DE L'OUEST: Cul de Sac east of Gautier, *Holdridge 1241* (GH, US), *1166* (GH, US); Fond Parisien, Étang Saumatre, *Leonard 4056* (C, GH, NY, US); Montagnes du Trou d'Eau, Morne à Cabrits, *Ekman H-1023* (A, S); Massif des Matheux, Magasin Carriès, *Ekman H-3302* (A, S, US).

The habit of this plant in the field is strikingly different from all other species of *Coccoloba* which I have encountered. The plant occurs as a low shrub in arid regions, especially in thorn-shrub zones. There is no single trunk to the plant, but numerous branches arise in a cluster and each branch-system arches. The lateral branches from the shoots are all arranged on two sides of the stem so that the aspect of the plant is of flattened leafy shoots.

There were no signs of damage to these plants seen in the field. Although the habit of the plant suggested that it consisted of adventitious shoots, no evidence of a central trunk was found. While all growth was slow on the plant, a few branches showed signs of more vigorously growing twigs. These possessed slightly longer internodes and leaves around 1 cm. in diameter. This relatively small-sized leaf blade was in contrast to the even smaller leaves of the rest of the plant. The secondary branches are

characteristically short shoots of extremely slow growth with compacted nodes and no internodal regions.

The sterile herbarium specimens of *Coccoloba subcordata* are difficult to distinguish from the adventitious shoots of *C. leoganensis*. The flattened branches and the short shoots, as well as the petiole arising from the apex of the ocrea, enable one to distinguish this species from the adventitious shoots of *C. leoganensis* either in the field or in the herbarium, however.

The similarity in appearance of these two species is disturbing. *Coccoloba subcordata* was originally described by De Candolle as a questionable species of *Erythroxylon* and was based on a Bertero specimen. Martius (Abhdl. Bayr. Acad. 3: 303. 1841) suggested the correct affinity for the plant and Lindau transferred the species, publishing the new combination. Interestingly enough, several of the specimens cited above had been incorrectly referred to the genus *Erythroxylon*.

Coccoloba swartzii Meisner, DC. Prodr. 14: 159. 1856; Lindau, Engl.

Bot. Jahrb. 13: 157. 1890; Howard, Jour. Arnold Arb. 30: 420.

1949, 37: 317-339. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisner, DC. Prodr. 14: 160. 1856.

Coccoloba barbadensis Lindau, Engl. Bot. Jahrb. 13: 148. 1890, not Jacquin.

Coccoloba diversifolia Lindau, Symb. Antill. 1: 223. 1899, and most recent authors, not Jacquin.

Trees 24 to 60 feet tall, branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ocreae 10-12 mm. long, the basal portion 3-5 mm. long, coriaceous, persistent, the upper portion membranaceous and deciduous, puberulent to glabrate; leaves of normal shoots with petioles 10-18 mm. long, puberulent or glabrate, the blades ovate to elliptic, 2.2×1.3 , 7×5 , 11×9 , 15×7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, having pit-like depressions on the upper surface and small glands on the lower surface, the apex acute, often rounded, the base narrowed, rounded or slightly cordate and usually oblique, the margin entire; midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate, anastomosing, the secondary venation conspicuous, reticulate; leaves of adventitious shoots with petioles 1.5-2.5 cm. long, the blades generally ovate to lanceolate 23×8.5 , 45×18.5 , to 70×25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescences terminal, 10-15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3-5 flowers at each node, tightly surrounded by membranaceous ocreolae which form a truncate cylinder after the flowers have fallen, the pistillate flowers borne singly at each node, the bracts ovate, 0.5 mm. long, the ocreolae 1-1.5 mm. long, membranaceous, the pedicels shorter than the ocreolae; hypanthium 0.5 mm. long, the perianth lobes 1-1.5 mm. long, the fertile stamens 1-1.5 mm. long, the sterile stamens rudimentary, 0.5 mm. long; fruit ovoid, 8-10 mm. long, 6

mm. diameter, the perianth lobes 1–1.5 mm. long and coronate in fruit; the achene dark brown.

DISTRIBUTION: Jamaica, Bahamas, Dominican Republic, Puerto Rico, St. Croix, St. Jan, Virgin Gorda, St. Thomas, Saba, St. Kitts, Montserrat, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia and Barbados.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: San Isidro, *Ekman H-11014* (A, S, US). PROV. PUERTO PLATA: Puerto Plata, *Wright, Parry and Brummel 472* (GH, US), *473* (GH, US). PROV. TRUJILLO: Villa Altagracia, *Taylor 414* (NY), *431* (NY, US), *433* (B, NY, US).

A full discussion of the variation in form of this species and the correct application of the names *Coccoloba barbadensis*, *C. diversifolia* and *C. swartzii* was published as the second paper of this series (Jour. Arnold Arb. 37: 317–339. 1956). If the var. *portoricensis* were recognized, the specimens seen from the Dominican Republic would be referred there. However, gradation from Puerto Rico to Jamaica, including this outlying population in the Dominican Republic, does not warrant the recognition of Meisner's variety.

***Coccoloba uvifera* L. Syst. Nat. ed. 10. 1007. 1759.**

Polygonum uvifera L. Sp. Pl. 365. 1753.

Guaiabara uvifera House, Amer. Midl. Nat. 8: 64. 1922.

Tree of strand areas, 6–50 feet tall, the branches terete, stout, papillose to pilose, the nodes not tumid; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, papillose to pilose; leaves of normal shoots with petioles stout, 7–10 mm. long, papillose to pilose, the blades orbicular to reniform, 6×8 , 11×13 , 13×18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extending around the petiole, the midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; leaves of adventitious shoots usually variable in size and shape, commonly obovate; inflorescences stout, 15–30 cm. long, the rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary at each locus, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ocreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long; fruit obpyriform, 1.2–2 cm. long, 8–10 mm. in diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, the perianth rose-purple when mature, the achene black.

LOCAL NAMES: *Raisin la mer* (H), *Uva caleta*, *Uva de mar*, *Uvero de playa*, *Uva de playa* (DR).

DISTRIBUTION: Along the shores of Florida, Bermuda and through the Caribbean Islands to Mexico, Central and South America. Spontaneous in Africa and the Pacific Islands.

Dominican Republic. PROV. LA ALTAGRACIA: Punta Macao, *Howard* 9767 (A); east of Jovero, *Abbott* 2878 (US); Llano Costero, Jaina, *Ekman* 19475 (US). PROV. BARAHONA: Barahona, *Fuertes* 247 (US), 1143 (F, GH, US); Beata Island, *Howard* 12489 (GH); Alta Vela Island, *Howard* 12453 (GH); El Caiman near Enriquillo, *Howard* 12188 (GH), 12191 (GH). PROV. MONTE CRISTI: Los Siete Hermanos, Monte Grande, *Howard* 12523 (GH). PROV. SAMANÁ: Samaná *Abbott* 1187 (US).

Haiti. DEPT. DU NORD OUEST: Port de Paix, *E.C. & G.M. Leonard* 11169 (A, GH, US); Ile de la Tortue, La Vallée, *Leonard* 11701 (US). DEPT. DU NORD: Bayeux near Port Margot, *Nash* 907 (NY). DEPT. DE L'OUEST: Petit Gonave Island, *Leonard* 5239 (GH, US); Morne a Bateau, Port-au-Prince, *Ekman* 8162 (S, US).

This common strand plant is certainly more abundant in Hispaniola than the collections cited above would indicate. It is also commonly cultivated as an ornamental shrub or tree.

Coccoloba uvifera L. \times *Coccoloba pubescens* L.; *Howard. Jour. Arnold Arb.* 36: 225. 1955.

Shrub or tree to 18 feet tall with habit of *Coccoloba uvifera*, i.e., some branches erect, some branches semi-prostrate; branchlets terete, sulcate when dry, pubescent or puberulent, the nodes slightly enlarged; ocreae to 1 cm. long, deeply cleft, the basal portion persistent; leaves of normal shoots with petioles to 1 cm. long, puberulent or pubescent, attached at the bases of the ocreae; blades usually orbicular, 8.5×9.5 , 11×14 , 12.5×13 , 15×19 cm. long and broad, thick or fleshy, plane or slightly bullate, drying yellow-green in color, short pubescent on the midrib and primary veins above, the rest glabrous, persistently short pubescent on the veins below, the lower surface dark-glandular-dotted, the apex rounded, occasionally broadly and shortly mucronate, the base cordate, the lobes overlapping, the margin entire, slightly undulate, the primary veins usually 5 pairs, impressed above, arcuate and conspicuously anastomosing near the margin; adventitious shoots with ocreae 1–2 cm. long, the leaves with petioles to 1 cm. long, stout, the blades broadly orbicular or slightly rhombic, 22×24 to 27×36 cm. long and broad, otherwise as in mature shoot leaves; inflorescences 12–25 cm. long, terminal and generally paired, with one raceme shorter than the other, the rachis puberulent; staminate flowers not seen; pistillate flowers 3–10 at each locus, these seemingly scorpioid in development, the bracts triangular, to 1 mm., the ocreolae membranaceous, 1 mm. long, the pedicels to 2.5 mm. long, puberulent, the hypanthium short, to 0.5 mm. long, the perianth lobes ovate, 1.5–2 mm. long, 1–1.5 mm. wide in bud, the stamens rudimentary, the anthers

abortive, the pistil 1.5–2 mm. long; fruit obovoid, 12–13 mm. long, 6–7 mm. diameter, narrowed to a short stalk-like base 2–3 mm. long, the apex rounded, the fleshy perianth lobes imbricated, red; achene obovoid to globose, light brown, smooth or slightly pitted.

Dominican Republic. PROV. BARAHONA: El Caiman between Enriquillo and El Can, *Howard 12189* (GH), *12191* (GH); Beata Island, *Howard 12499* (GH).

Haiti. DEPT. DU SUD: Miragoane, *Eyerdam 397* (GH, NY, US); Anse à Veau, *Picarda s.n.* (GH).

In 1950 Mr. George Hamor of Barahona discovered an unusual stand of *Coccoloba* along a coral shelf and rocky beach area south of Barahona. He later arranged transportation to the spot and showed me this definite hybrid. The plant described here occurs between a coastal stand of *C. uvifera* (*Howard 12188*) and an inland stand of *C. pubescens* (*Howard 12187*). Fully a dozen mature plants were found in this location. Not only is the plant intermediate in geographic location, but all of its characteristics show its hybrid origin from *C. uvifera* and *C. pubescens*. In habit the plant resembles *C. uvifera*, being a plant of low stature with some branches semi-prostrate and spreading while others are erect, giving each plant the definite clump-like appearance of *C. uvifera*. The leaf shape of the normal leaves on mature branches is that of *C. uvifera* except in texture, in which they resemble *C. pubescens*, having the conspicuous reticulate venation on the lower surface. The pubescence of the leaves combines that of the parent species. The leaves of the adventitious shoots more closely resemble those of *C. pubescens* in size, shape and aspect than comparable leaves of *C. uvifera*. In the arrangement of the flowers and the pubescence, the characters remind one of *C. pubescens*, although the presence of a smaller raceme arising laterally from the base is more common in *C. uvifera*. Only female flowers are known. The fruits are smaller than typical *Coccoloba uvifera* but resemble them in shape and are unlike those of *C. pubescens*. Fruits were abundant on the hybrid plants and appeared in the field to be fully developed. However, none of the one hundred fruits collected would germinate a month later, while eighty per cent germination was obtained from a collection of *C. uvifera* made at the same time.

A similar stand of the hybrid was found on Beata Island two weeks later and again both parents were present.

The collection *Eyerdam 397* is referred to this new hybrid. The specimen appears to have been taken from adventitious shoots and possesses larger leaves more closely resembling *Coccoloba pubescens*. As is generally true of flowering material collected from adventitious shoots, the inflorescence of this specimen is larger, approaching 35 cm. in length.

While the suggested hybrid origin of *Coccoloba antiguensis* Sandwith from Antigua has been rejected and that species referred to the synonymy of *C. pubescens*, there is no doubt in my mind as to the valid nature and the origin of the present hybrid. The hybrid nature of this collection is obvious in the field and equally so in the specimens cited.

The other hybrid plants and populations involving *Coccoloba uvifera* considered in this paper are *C. costata* \times *C. uvifera*, *C. hotteana* \times *C. uvifera* and *C. krugii* \times *C. uvifera*.

Coccoloba venosa L. Syst. Nat. ed. 10. 1007. 1759; Fawcett and Rendle, Jour. Bot. 51: 123. 1913.

Coccoloba punctata L. Sp. Pl. ed. 2. 523. 1762.

Uvifera arbor americana, fructu aromatico punctatus, Pluk. Alm. 394, t. 237, fig. 4. 1696, as to leaf only.

Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, pl. 78. 1763; Enum. Pl. 19. 1762.

Guaibara venosa House, Amer. Midl. Nat. 8: 64. 1922, as *Guaibara*.

Trees to 45 feet tall; branches terete, glabrous, the nodes not tumid; ocreae membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long, glabrous or with flattened glands; leaves of normal shoots with petioles 5–10 mm. long, glabrous, the blades oblong-lanceolate to elliptic, 8×4 , 10×4.5 , 16.5×6.5 , 21×9 , 27×10.5 cm. long and broad, membranaceous, glabrous except for clusters of hairs in the axils of the veins, sparsely glandular below, the apex short-acuminate, the base narrowed and slightly cordate or cuneate or obtuse, the midrib and primary veins slightly prominent on both surfaces, the primary veins 8–13 pairs, straight or arcuate, bifurcate and anastomosing at the margins; leaves of the adventitious shoots about the same size, the internodes much elongate and the ocreae to 4 cm. long; inflorescences terminal or terminal on short lateral branches, the rachis puberulent, angular; staminate flowers in clusters of 2–5, the pistillate flowers solitary, the bracts lanceolate-ovate, to 1.5 mm. long, black, puberulent to pilose or commonly with a fringe of hairs at the apex; ocreolae to 2 mm. long, membranaceous, enlarging with the expanding bud, each flower with an ocreola, the flowering pedicels 1–2 mm. long, glabrous; hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5–2 mm. long and broad, slightly unequal, the fertile stamens to 1 mm. long; fruiting pedicels 1.5–2.5 mm. long, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit broadly ovoid, 3–4 mm. long and broad.

DISTRIBUTION: Cuba (introduced), Hispaniola, Puerto Rico, Jamaica (?), Virgin Islands, Lesser Antilles and Trinidad.

Dominican Republic. DISTRICT DE SANTO DOMINGO: between Ciudad Trujillo and La Caleta, *Ekman H-14231* (s). PROV. LA ALTAGRACIA: Llano Costero at La Romana, *Ekman H-12089* (b, s). PROV. SAMANÁ: Cabo Samaná near Puerto Colorado, *Ekman H-15333* (s). PROV. SEIBO: Monte Redondo, east of Jovero, *Abbott 2792* (b, us). PROV. UNKNOWN: Cupey, *Eggers 2682* (ny, us).

Haiti. DEPT. DU NORD OUEST: Ile de la Tortue, La Vallée, *Ekman H-9758* (s, us). DEPT. DU NORD: Massif du Nord, Port Margot, Bayeux, *Ekman H-2699* (s, us). Without specific location: *Sessé & Mocino 952* (f), *5431* (f).

Coccoloba wrightii Lindau, Engl. Bot. Jahrb. 13: 151. 1890; Howard, Jour. Arnold Arb. 30: 418. 1949.

Coccoloba scrobiculata Lindau, Engl. Bot. Jahrb. 13: 140. 1890.

Coccoloba subtruncata Urban, Symb. Antill. 7: 211. 1912.

Coccoloba saxicola Britton, Bull. Torrey Bot. Club 50: 37. 1923.

Shrub or small tree to 21 feet tall; branches terete, the nodes not swollen, glabrate; ocreae membranaceous, 4–6 mm. long, puberulent to tomentose or glabrate; leaves of normal shoots with petioles 4–7 mm. long arising from the bases of the ocreae, the blades ovate, elliptic, obovate or rarely ovate-lanceolate, 5×2.5 , 8×4 , 10×7 to 11×10 cm. long and wide on mature shoots, coriaceous, umbonate between the veins, shining above when young but dull on both surfaces when mature, the apex acute to abruptly short acuminate or truncate, the base narrowed to obtuse, usually slightly oblique, the primary veins 4–6 pairs, arcuate, impressed above, conspicuous below, the lower surface more or less dotted with stomatal excretions; adventitious shoots with ocreae to 2 cm. long; leaves with petioles 2.5 cm. long, the blades broadly ovate to elliptic, 15×14 to 20×17 cm. long and broad, the apex of these leaves rounded to obtusely short mucronate, the bases rounded to subcordate; inflorescences terminal, 3–10 cm. long, the rachis pubescent or with resinous excretions, the bracts ovate, to 0.5 mm. long, the ocreolae membranaceous, 1 mm. long, the flowering pedicels 1 mm. long, increasing in length either in fruit or after staminate flowers have fallen to 3 mm.; staminate flowers 2–3 per locus, the pistillate flowers borne singly at each locus; hypanthium to 1 mm. long, the perianth lobes 1–1.5 mm. long and broad, the fertile stamens united at the base for 1 mm., the free portions 0.5–1 mm. long, the sterile stamens less than 1 mm. long, the functional pistil to 2 mm. long; fruit ovoid, slightly contracted at the base, rounded but only slightly coronate at the apex, 7–9 mm. long, 4–5 mm. in diameter.

DISTRIBUTION: Cuba and Hispaniola.

Dominican Republic. PROV. BAHORUCO: between El Aguacate and Pedernales. *Howard* 12585 (GH). PROV. LA VEGA: Constanza, *Türkheim* 3304 (B-type of *C. subtruncata*, F, GH, M, MO, NY, S, US); Arroyo Pantufo near Constanza, *Ekman* H-14089 (A, S, US); Bonao, *Ekman* 16450 (S, US). Without specific location: *Schomburgk* 123 (B), *Preneloup* 492 (B, US), *Bertero* s.n. (B).

Coccoloba scrobiculata Lindau was described, collections by Schomburgk and Preneloup being cited, in the same publication as *C. wrightii* Lindau. Lindau attempted to distinguish between them in a key by indicating that the lesser venation was flat and inconspicuous above in *C. scrobiculata* while it was more prominent in *C. wrightii*. This is scarcely a reliable characteristic in the genus and I have no doubt that only one species is involved. No recent collections have been referred to *C. scrobiculata* and I have chosen to accept the better known and documented *C. wrightii* as the species. Although *C. scrobiculata* was described a few pages earlier, but at the same time as *C. wrightii*, I am considering it a new synonym. The

venation pattern of material called *C. scrobiculata* by Lindau is easily included in the range of variation of *C. wrightii* and in all characteristics visible in the scanty flowering material, the two are identical.

Coccoloba subtruncata, described some years later by Urban, was based on a collection made near Constanza by H. von Türckheim. The species has been recollected in the same area by Ekman and additional collections are available from other areas. Urban's original diagnosis was presumably based on the one sheet of the Türckheim collection in the Berlin herbarium. I have on loan nine sheets of this number which are obviously the same but which would necessitate a new description to be accurate. Recent material (e.g., Ekman H-16450 and H-14089) in fruit allows a complete diagnosis of this species which obviously is the same as *Coccoloba wrightii* of Cuba and must be referred to synonymy there. In general, the Hispaniolan specimens have less pubescence when mature than do the Cuban plants. However, the type collection of *C. subtruncata*, in spite of Urban's description, exhibits the same pubescence as *C. wrightii*, at least on the young shoots and the tips of the ocreae. *Coccoloba wrightii* has been considered to be endemic to Cuba, but its range is now extended to the Dominican Republic and specimens should be found in Haiti.

A twisted tree represented by Howard 12585 was alongside a new road from El Aguacate to Pedernales in the Dominican Republic. In the course of road-building this tree had been pushed over at an angle and from the lower portion erect adventitious shoots had developed with large and extremely thick-coriaceous leaves. These adventitious stems were 8–10 mm. thick near the apex in contrast with the much smaller diameter of the normal growth. The largest leaves on the shoot had stout petioles 2–2.5 cm. long and broadly ovate to elliptic leaves to 19×15 cm. long and broad. The apex of the blade was rounded to short and obtusely mucronate and the bases were rounded to subcordate. The terminal portions of this plant produced shoots which were identical with those in the type collection of Türckheim. Similar-sized leaves of adventitious shoots of *Coccoloba wrightii* have already been reported and the previous description is amended only to include leaves which are rounded to subtruncate at the base.

The collection Ekman H-15135 from Los Bañaderos Prietos near Laguna on the Samaná Peninsula was named by Schmidt as "*C. subtruncata* forma." Ekman's field notes state, a "small tree, alas, sterile." This material seems more appropriately referred to *Coccoloba pauciflora* Urban. It is obviously from adventitious shoots and the normal foliage is not represented. Neither *C. pauciflora* nor *C. wrightii* has been reported from the Samaná Peninsula.

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With four plates

Subgenus VII. *Botryanthus* Webster, Jour. Arnold Arb. 37: 345. 1956.

Trees or shrubs with non-phyllanthoid branching, the leaves on the main axes not reduced to scales, ultimate axes not regularly deciduous. Monoecious; flowers borne in thyrses or axillary clusters. Male flower: calyx-lobes 5 or 6; disk-segments 5 or 6, often massive; stamens 3, filaments connate, anthers dehiscing horizontally or obliquely; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6; disk cupuliform; ovary of 3 carpels, smooth; styles erect or spreading, usually connate (at least basally) into a column, the tips entire to bifid. Fruit capsular, sometimes very large; seeds trigonous, essentially smooth.

Subgenus *Botryanthus* is an entirely Neotropical group which includes possibly 35 species, most of these occurring in Central and South America. In addition to the dubious sect. *Diplocicca* from Brazil (based on *P. octomerus* Muell. Arg.), other South American sections may eventually be defined; but the majority of the species in the subgenus (including all the West Indian ones) clearly are referable to sect. *Elutanthos*.

From the phylogenetic point of view subg. *Botryanthus* is of especial interest because it is closely related to subg. *Xylophylla*. Its areolate pollen grains are essentially identical to those of the latter subgenus and, since its branching is non-phyllanthoid (and hence presumably unspecialized), subg. *Botryanthus* might logically be considered the ancestral group. The reduction series in inflorescence within sect. *Elutanthos* (which can be traced from the elaborate "panicle" of *P. grandifolius* to the axillary flowers of *P. nutans* ssp. *grisebachianus*) could furthermore be cited in support of such a supposition. On the other hand, it must be noted that in many ways *P. grandifolius* is a very specialized plant, for it has capsules and seeds extraordinarily large in the genus, and its male flowers with three connate stamens give no indication of primitiveness. A rather convincing argument could be put forth to read the phylogeny in precisely the opposite direction, and to assume that subg. *Botryanthus* has evolved from some group within subg. *Xylophylla* (such as sect. *Asterandra*) by a regression from phyllanthoid to non-phyllanthoid branching. Such a hypothesis would involve the assumption that a great increase in leaf and fruit size (such as occurs in *P. grandifolius*) would place a selective advantage on any reversion from deciduous to permanent reproductive axes. At present a decision for either of the alternative hypotheses can-

* Continued from volume XXXVIII, p. 373.

not be made, but with the accumulation of additional evidence (particularly from cytology) it should be possible to do so.

Sect. 15. *Elutanthos* Croiz. Jour. Wash. Acad. Sci. 33: 12. 1943.

Shrubs or trees with unspecialized ramification, leaves distichous on persistent axes. Monoecious; flowers in cymules in the axils of foliage leaves or of bracts (the inflorescence then thyrsoid), or sometimes solitary. Male flower: calyx-lobes 6; disk-segments 6, often massive; stamens usually 3, filaments completely united into a column; anthers dehiscing more or less horizontally (or deflexed); pollen grains globose, areolate, the areoles usually polybrochate. Female flower: calyx-lobes 6; disk patelliform; styles erect, connate at least below, entire to bifid. Capsule obscurely rugulose; seeds smooth.

TYPE SPECIES: *Phyllanthus glaucescens* H.B.K. [= *P. grandifolius* L.].

As established by Croizat, sect. *Elutanthos* included seven species of Central and South America; but there are undoubtedly a number of others which are to be referred here, including the following six species from the West Indies. The West Indian plants differ from the mainland *P. grandifolius* and its allies in their smaller capsules and less elaborate inflorescence, but the similarities are so striking that there is obviously a close affinity.

The combination of an indefinite branching pattern and usually raceme-like inflorescence distinguishes the species of sect. *Elutanthos* from all other woody West Indian species. However, the expression of inflorescence is quite variable and the typical thyrses are not developed in *P. nutans* ssp. *grisebachianus* and some forms of *P. nutans* ssp. *nutans*. Where the raceme-like thyrses occur, they often appear to be terminal, but close inspection will show that each thyrses does not represent a continuation of the branch axis but is rather inserted just below the abortive tip of the axis; often an additional thyrses is produced at one or more additional nodes below. In addition, cymules may also occur in the axils of foliage leaves; in such cases, these axillary cymules tend to be male and the ones in the "racemes" female. The homology between the more or less naked thyrses and the leafy branch-ends is as ill-defined as that between branch-orders, for the degree of distinctiveness of thyrses development is at least partially dependent on the vigor of the branches. Sometimes there may be long "leader" shoots which bear short thyrsiferous branchlets in distichous order, but in other instances the thyrsiferous branchlets may themselves be of the penultimate order and produce additional leafy axes as well as "racemes" of flowers.

Ecologically the West Indian representatives of sect. *Elutanthos* are characterized by a xerophytic tendency, most of the species appearing to grow in open scrub formations at low altitudes. The widespread *P. nutans*, however, occurs in a considerable variety of habitats, including some of the wettest rain forest in Jamaica.

KEY TO THE SPECIES

1. Calyx-lobes of male flowers less than 1.5 mm. long; capsules trigonous; plants of the southern Caribbean.
 2. Styles subentire (truncate-emarginate), completely erect and connivent (with no reflexed portions); disk of female flower extremely massive; plants completely glabrous; Curaçao. 43. *P. botryanthus*
 2. Styles with bifid sharply reflexed tips; disk of female flower tenuous; branchlets and inflorescence axes hirsutulous; Barbados. 44. *P. anderssonii*
1. Calyx-lobes of male flowers over 1.5 mm. long; capsules rounded; plants of the northern Caribbean.
 2. Staminal column with 3 apiculae alternating with the anthers; leaf-blades densely hirsutulous beneath, sparsely hirsutulous above; style-tips entire or merely emarginate; Haiti. 47. *P. urbanianus*
 2. Staminal column without apiculae; leaf-blades glabrous or sparsely hirsutulous beneath, glabrous above; styles definitely bifid.
 3. Leaf-blades rigidly coriaceous, the main veins distinctly sunken above; stipules indurate, dark and shiny, colored as the branch; Cuba. 46. *P. pachystylus*
 3. Leaf-blades chartaceous, the veins not sunken above; stipules not indurate; Jamaica and Cuba. 45. *P. nutans*
43. *Phyllanthus botryanthus* Muell. Arg. in DC. Prodr. 15(2): 323 1866. (PLATE XXIV, figs. A-B).

Diasperus botryanthus (Muell. Arg.) O. Ktze. Rev. Gen. 2: 598. 1891.

Phyllanthus euwensii Bold. Fl. Dutch W. Ind. 2: 50-51, pl. 4. 1914.

Glochidion botryanthum (Muell. Arg.) Pax & Hoffm. Naturl. Pflanzenfam. ed. 2, 19c: 58. 1931.

Glabrous shrub or small tree c. 1-4 m. high; branches slender, terete, furrowed, reddish-brown, c. 1.5-4 mm. thick; leader shoots up to 25 cm. long, lateral branchlets (of current year) c. 3-20 cm. long, with 5-15 leaves. Leaves: stipules triangular, mostly 0.8-1.1 mm. long and 0.5-0.6 mm. broad, acute, scarious, reddish- or blackish-brown, persistent (at least the basal portion), more or less entire. Petioles dark, grooved above, angled, 2.5-4 mm. long. Leaf-blades membranous or chartaceous, mostly ovate, c. (3-) 4.5-7.5 cm. long, (2-) 2.5-5 cm. broad, acute or obtuse (rarely emarginate) at the tip, obtuse or rounded at the base; above darkened in drying, the midrib and laterals very slightly raised; beneath more or less pruinose, the midrib salient, the laterals (c. 6-8 on a side) arching, slightly raised, branching to form a reticulum; margins unthickened, plane.

Monoecious; flowers mostly in bisexual cymules on leafless thyrses at distal nodes of ultimate axes; female flowers usually 1 or 2, males 3-6 per cymule, or the sexes more or less segregated onto different thyrses.

Male flower: pedicel capillary, c. 1 cm. long. Calyx-lobes 6, subequal, elliptic-oblong, c. 1-1.2 mm. long and 0.5-0.8 mm. broad, obtuse, purple-

stained except for the narrow scarious entire margins, midrib unbranched or nearly so. Disk-segments 6, massive, subcubical, foveolate, c. 0.3–0.4 mm. broad. Stamens 3; column c. 0.35–0.4 mm. high; anthers sessile, discrete, triangular, acute, c. 0.25–0.35 mm. long, 0.35–0.4 mm. broad; anther-sacs divergent, the slits not confluent, dehiscing horizontally; pollen grains mostly 22–26 μ in diameter, areoles oligobrochate, c. 5 μ across.

Female flower: pedicel capillary, (10–) 13–16 (–19) mm. long. Calyx-lobes 6, triangular-oblong, c. 1.2–1.3 mm. long and 0.7–0.8 mm. broad, acute or subacute, purple-stained as the male, the narrow scarious margin more or less entire, the midrib sparingly branched. Disk convex, extremely massive, circular or angled, nearly 2 mm. across, foveolate. Styles erect, connate or coherent into a column 0.3–0.45 mm. high, slightly dilated and merely truncate-emarginate at the apex.

Capsule oblate, trigonous, c. 3 mm. high and up to 6 mm. broad, somewhat rugulose, the veins obscure or conspicuous. Columella 1.7–2 mm. high. Seeds plano-convex, plump, umbonate (heliciform), 3.3–3.6 mm. long, 2.7–2.9 mm. broad, light brown, smooth (finely striolate).

Collected in flower and fruit May to January.

TYPE: Colombia, Carthagená, *Triana 3664* (P, LECTOTYPE; K, W, ISOTYPES).

DISTRIBUTION: coastal plain, northern South America (MAP XVIII).

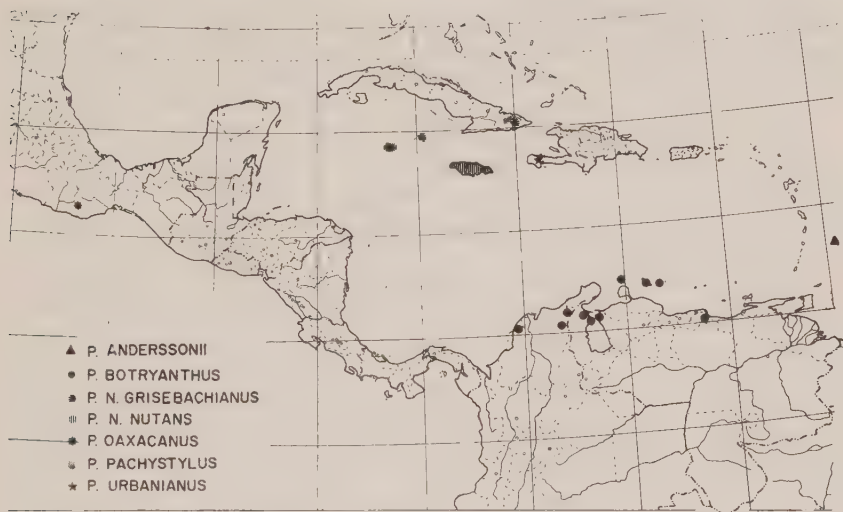
ARUBA: Kristalberg, 1885, *Suringar* (L). CURAÇAO: road near Antonyberg, *Boldingh 5141* (C); road near Wacao, *Boldingh 5252* (L); calcareous soil near San Pedro, *Boldingh 5279* (NY, ISOTYPE of *P. euwensii*); Tafelberg, *Curran & Hamman 164* (A); Hofje Abau, *Curran & Hamman 180* (A); rif-hospitaal, Hato, Savonet, *Suringar* (L). BONAIRE: klip Slachtbaai, *Suringar* (L). (Additional localities cited by Boldingh, loc. cit.)

The Curassavican plants represent merely a small outlying population of this species which is widespread and common in lowland areas along the northern coasts of Colombia and Venezuela. The specimens from the Dutch islands show no evident differences from the mainland plants, so that Boldingh's proposed *P. euwensii* cannot be maintained even at subspecific rank. Boldingh did not give any distinguishing characters for his intended new species, nor did he discuss its relationships; apparently he was unaware that the species also occurred on the mainland or that it had already received a name.

Because of its essentially entire styles associated in a column, *P. botryanthus* was placed by Mueller in his artificial sect. *Hemiphyllanthus*; it was therefore one of the species transferred to *Glochidion* by Pax and Hoffmann (loc. cit.), who arbitrarily assigned all species of *Phyllanthus* with entire styles to *Glochidion*. This betrayed mere bibliographic acquaintance with the plants, for *P. botryanthus* and *P. ovatus* (the other West Indian representative of Mueller's sect. *Hemiphyllanthus*) are neither closely related to one another nor to species of *Glochidion*.

The habit, floral structure, and pollen grains of *P. botryanthus* together

indicate an unquestionable relationship with the other species of sect. *Elutanthos*. Within the section, the closest West Indian relation appears to be *P. anderssonii*, which has very similar vegetative parts and male flowers but utterly different female flowers with bifid reflexed styles and a tenuous disk. In contrast, the female flowers of *P. botryanthus* are distinguished by the subterre erect styles and extraordinarily massive disk, which even in the bud stage is massive and swollen and which expands precociously to cause the calyx-lobes to become reflexed. However, the Mexican *P. oaxacanus* has a similar massive disk and, despite its very different styles, is probably the most closely related species.



MAP XVIII. Distribution of some Caribbean species of sect. *Elutanthos*.

44. *Phyllanthus anderssonii* Muell. Arg. in DC. Prodr. 15(2): 395. 1866 (as *P. anderssoni*). (PLATE XXIV, figs. C–D).

Phyllanthus barbadensis Urb. Symb. Ant. 3: 287. 1902.

A shrub c. 1 m. high [ex Eggers], with slender leader shoots up to c. 30 cm. long bearing distichous branchlets which terminate in naked thyrses (or leaders serving directly as thyrses-bearing axes); ultimate axes (branchlets) reddish brown, terete, sparsely to rather densely hirsutulous, mostly 4–10 cm. long, 0.6–1 mm. thick, with c. 6–15 nodes. Leaves: stipules triangular-lanceolate, 0.75–1 mm. long, 0.3–0.5 mm. broad, acute or acuminate, more or less hirsutulous, scarious, becoming reddish brown and at least the base persistent, entire or denticulate. Petioles dark and slender, flattened and hirsutulous adaxially, convex and glabrous abaxially, 1–1.8 mm. long. Leaf-blades membranous or chartaceous, elliptic to mostly ovate, c. 2.5–4.5 cm. long, 1.2–2.5 cm. broad, obtuse or subacute at the tip, cuneate at the base; above olivaceous or drying blackish,

hirsutulous proximally on the midrib but otherwise smooth and glabrous, nerves slightly raised; beneath glabrous, pale or pruinose, the midrib distinctly raised, the laterals (c. 7–10 on a side) ascending, slightly raised, connecting intramarginally, the tertiaries forming a rather inconspicuous reticulum; margins scarcely thickened, plane.

Monocious; cymules mostly unisexual; male cymules several-flowered, borne at proximal axils of branchlet usually axillary to foliage leaves; female cymules with 1–4 flowers, borne on the thyrsiform terminal portions of branchlets (the leaves becoming more or less abruptly reduced to scales); one or two cymules at the transitional region often bisexual.

Male flower: pedicel capillary, up to c. 8 mm. long. Calyx-lobes 6, chartaceous, subequal, elliptic to oblong or obovate, c. 1–1.3 (–1.5) mm. long, 0.75–1 mm. broad, obtuse or subacute, entire or obscurely crenulate, the midrib unbranched. Disk-segments 6, very massive (about as large as the anthers), deeply furrowed and pitted, c. 0.3–0.4 mm. broad. Stamens 3; column c. 0.5–0.7 mm. high, c. 0.25 mm. thick; anthers sessile atop the column, discrete, the common connective convex, c. 0.2–0.3 mm. long and 0.35–0.4 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21–25 μ in diameter, areoles polybrochate, c. 5–7 μ across.

Female flower: pedicel slender, 7–13 mm. long. Calyx-lobes 6, subequal, ovate-oblong or obovate, 1–1.4 mm. long, 0.7–0.9 mm. broad, rounded or subtruncate at the tip, entire or obscurely crenulate, the midrib sparsely branching. Disk cupuliform, enclosing up to $\frac{1}{3}$ of the ovary, the tenuous rim crenulate, pitted. Styles connate or loosely coherent into a column c. 0.4–0.7 mm. high, the free ends sharply reflexed, bifid up to $\frac{2}{3}$ their length, the tips subulate, obtuse and entire or again emarginate or bifid.

Capsule oblate, trigonous, 6-sulcate, dark purplish brown, obscurely venose, c. 5.5–6 mm. broad, the valves c. 4.5 mm. long. Columella 1.8–2 mm. high. Seeds plano-convex, plump, umbonate, 2.7–3.3 mm. long, 1.7–2.3 mm. radially, 1.8–2.4 mm. tangentially, pale brown with very irregular longitudinal bands of slightly raised transversely elongated reddish-brown cells; hilum submedian.

Collected in flower Jan., Feb., June, Nov.; in fruit Feb., Nov.

TYPE: "Caracas," collector unspecified (Prodromus Herbarium, G, HOLOTYPE). The typification of this species is unfortunately fraught with difficulties which at this time cannot be wholly resolved. In Mueller's original description the origin of the type collection was indicated as follows: "Prope Caracas (hb. holm. sub n. 288! a cl. Dr. Andersson miss.)." Presumably the specimen was not collected by Andersson, since during his trip on the "Eugenie" he did not visit anywhere within the Caribbean area, his closest approach being the Pacific coast of Panama (cf. end-map in Skogman, Fregatten Eugenie Resa Omkring Jorden. 1854–55). If the plant was really collected near Caracas it seems unlikely that it could have escaped notice subsequently, although this cannot be entirely ruled out. It appears more likely that the specimen was actually obtained on Barbados

but was subsequently mislabelled. A search through the literature indicates that there is at least one possible source of the collection, for Robert Schomburgk spent several months on Barbados in 1846-47 and his citation (Hist. Barbados 593. 1848) of *P. nutans* can hardly refer to any species other than the present one. The figure "222" for the citation in Schomburgk's list does not agree with the "288" cited by Mueller, but the latter might be a field number. Of course, none of these circumstances constitutes proof that Andersson's specimen is a duplicate of a Schomburgk collection, so that it is impossible to decide conclusively whether the type collection of *P. anderssonii* is from Venezuela or from Barbados. Although it differs in a few minor particulars, the type specimen of *P. anderssonii* corresponds so well (e.g., in its hirtellous axes, massive male disk-segments, and sharply reflexed styles) with the specimens of *P. barbadensis* that it must be conspecific; and Mueller's name must thus take precedence over the much later one of Urban.

DISTRIBUTION: endemic to Barbados (MAP XVIII).

BARBADOS: Lion Hill Gully, St. James, *Dash* 334 (NY); Forster Hall Wood, *Eggers* 7130 (A, GOET, US; LECTOTYPE COLLECTION of *P. barbadensis*); Cole's Cave, St. Thomas, *Freeman & Bovell* (NY); Highland Gully, St. Thomas, *McIntosh* (K); Jack-in-the-box Gully and under Hackleton's Cliff, *Waby* 15 (K); Bathsheba, *Warming* 27 (C).

Beard (Nat. Veg. Leeward & Windward Isl. 166. 1949) has pointed out that practically all of the natural vegetation on Barbados has disappeared and that many plants endemic to Barbados have become extinct. However, since *P. anderssonii* has been collected at a number of different localities up to 1935, it seems possible that it may still survive, even though Beard failed to encounter it in his own reconnaissance of the island.

Urban compared *P. anderssonii* (as *P. barbadensis*) with *P. nutans*, to which indeed it shows some similarities; but its closest relationship is undoubtedly with *P. botryanthus*. In the face of their present distributions, the affinity between *P. anderssonii* and *P. botryanthus* has some anomalous aspects. It seems curious, for instance, that the female flowers (which are the best distinguishing character) of *P. botryanthus* are much more highly modified than those of *P. anderssonii*, for one might expect that it would be the latter, which presumably has been derived by colonization from South America, that would show the greater specialization. It also seems surprising that no related forms occur in a gap of about 500 miles between the state of Miranda, Venezuela (the easternmost known station for *P. botryanthus*) and Barbados. One possible explanation is that *P. anderssonii* may represent a relict of an extensive population which occupied the ancient land-mass of "Paria"; according to Schuchert (Hist. Geol. Ant.-Car. Reg. 19. 1935) this region extended from Maracaibo to Barbados at some time during the Cenozoic, but later foundered and is now represented only by some of the off-shore islands of northern South America.

45. *Phyllanthus nutans* Sw. Prodr. 27. 1788; Fl. Ind. Occ. 1103. 1800; Muell. Arg. in DC. Prodr. 15(2) : 375. 1866; Fawc. & Rend. Fl. Jam. 4 : 253-254. 1920.

Diasperus nutans (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

A diffuse extremely variable shrub or slender tree 1-7 m. high, irregularly branching, the new axes borne distichously on older branches, often ending in nodding racemiform inflorescences, reddish brown, terete or angled, smooth or scabridulous or hirsutulous, 2-25 cm. long, 1-2.5 mm. broad, internodes 4-40 mm. long. Leaves: stipules scarious-chartaceous, deciduous or persistent, ovate to narrowly lanceolate, (2-) 3-5 (-9) mm. long, (1-) 1.5-4 (-6) mm. broad, obtuse to acute at the tip, truncate to cordate at the base, entire, yellowish, stramineous, or brownish. Petioles smooth or scabridulous to copiously hirsutulous, usually somewhat angled or margined, 1.5-4.5 mm. long. Leaf-blades chartaceous, quite variable in size and shape but most often ovate or elliptic, c. 3.5-8 (-11) cm. long, 2-5 (-8) cm. broad, obtuse or more rarely acute at the tip, cuneate to rounded at the base; above olivaceous, dull, the veins scarcely raised; beneath paler, sometimes glaucous or purplish-tinged, the midrib and lateral veins (5-8 on a side) raised, brownish or stramineous, the reticulum of veinlets usually conspicuous; margins unthickened, plane or revolute.

Monoecious; inflorescence variable; male cymules several-flowered, borne axillary or on pseudoterminal thyrses; female cymules 1-3-flowered, usually confined to the pseudoterminal thyrses (at least in ssp. *nutans*).

Male flower: pedicel capillary; 8-15 (-30) mm. long. Calyx-lobes 6, chartaceous, or somewhat fleshy, subequal, oblong to obovate, 2.3-3.2 mm. long, 1.3-2.2 mm. broad, rounded and obscurely crenulate or denticulate at the tip, often reddish at least below with thin creamy-yellow scarious margins but sometimes greenish throughout, the midrib with a few often conspicuous lateral branches. Disk-segments 6, thickened and fleshy, orbicular or reniform, obscurely to conspicuously foveolate-pitted, c. 0.35-0.7 mm. broad. Stamens 3; column c. 0.7-1.1 mm. high, tapering slightly to the apex; anthers sessile atop the column, discrete, usually deflexed but sometimes horizontal, broadly triangular to elliptic in outline, c. 0.4-0.6 mm. long and broad; anther-sacs slightly to markedly divergent, dehiscent horizontally or obliquely downwards, the slits confluent across the apex; pollen grains c. 21-26 μ in diameter, the areoles polybrochate, c. 6-8 μ across.

Female flower: pedicel terete, slender, smooth and glabrous or sometimes sparsely hirsutulous, reddish or olivaceous (sometimes pruinose), (6-) 10-27 mm. long. Calyx-lobes 6, erect at anthesis, biseriate, the outer elliptic-oblong and obtuse at the tip, the inner obovate and broader and more rounded at the tip; lobes 2-3.2 mm. long, 1-2.5 mm. broad, colored as the male, the scarcely raised midrib simple to conspicuously branched. Disk patelliform, fleshy, 6-angled or slightly lobed, foveolate. Styles erect, the undivided portions connate into a column 0.5-2.3 mm. high, the free

ends ordinarily sharply reflexed, bifid or parted nearly to the stylar column, the tips narrow or dilated, flattened, acute, 0.4–1.2 mm. long.

Capsule oblate-spheroidal, obscurely 6-ribbed, rounded in outline, c. 6 mm. high and 10 mm. broad, rugulose, the veins completely obscure. Columella c. 3–4 mm. high. Seeds trigonous (only slightly asymmetrical if at all), 4.2–7 mm. long, 2.8–4 mm. radially and tangentially, smooth, mottled light brown; hilum submedian.

Flowering probably throughout the year.

The populations of this extremely variable species of Cuba, the Cayman Islands, and Jamaica may be assigned to one or the other of the two following subspecies.

45a. *Phyllanthus nutans* ssp. *nutans* (PLATE XXIV, figs. E–F).

Phyllanthus nutans Sw. Prodr. 27. 1788.

Phyllanthus nutans β *purdiaeana* Baill. Adansonia 2: 15–16. 1862.

Phyllanthus nutans var. *trojanus* Webster, Contr. Gray Herb. 176: 47. 1955.

Stipules thin, usually precociously deciduous although conspicuous on young growth, ovate to lanceolate, (2–) 3–5 (–9) mm. long, (1–) 1.5–4 (–6) mm. broad, truncate or cordate at the base, glabrous, stramineous or greenish. Leaf-blades mostly ovate but often elliptic, glabrous beneath (except sometimes at the very base), usually obtuse or subacute at the tip and obtuse to rounded at the base; margins usually plane. Male cymules axillary or often at the proximal nodes of thyrses; female cymules 1–3-flowered, usually borne on more or less nodding pseudoterminal naked thyrses (i.e., ultimate axes with reduced leaves), sometimes the lowermost cymules in the axils of partially or wholly unreduced leaves. Calyx-lobes of male and female flowers subentire or obscurely denticulate, thickened at the base, the midrib simple or sparingly branched. Stylar column 0.5–2.3 mm. high; style-ends usually sharply reflexed, the lanceolate acute tips 0.4–1.2 mm. long.

TYPE: southern Jamaica, *Swartz*.

DISTRIBUTION: Jamaica and Cayman Islands (MAPS XVIII–XXI).

CAYMAN ISLANDS. GRAND CAYMAN: Grape Tree Point, dry rocky woodland, *Proctor 11977* (GH); between Old Isaacs and Wintersland, *Proctor 15245* (GH).

JAMAICA. Without locality: *Alexander* (A, GOET), *Hooker* (W), *Jacquin* (W), *Swartz* (S, HOLOTYPE; A, C, G, P, S, ISOTYPES), *Wilson 232* (NY), *Wulfschlaegel s.n.* (GH), 900, 1053, 1114 (GOET), 1318 (W). HANOVER: Fish River Mountains, *Britton & Hollick 2167, 2170* (F, NY), *Harris 10260* (F, NY, US); Dolphin Head, *Britton 2314* (F, NY), *Harris 10309* (F, US), *Webster & Wilson 5075* (A, JAM). WESTMORELAND: Negril, rocky wooded hills, *Britton & Hollick 2082* (NY). ST. JAMES: Chatham, alt. 300 m., *Guilbride & Barkley 221174* (MICH). ST. ELIZABETH: Potsdam woodland, *Harris 9778* (F, US); New Buildings, south of Gutters, *Howard & Proctor 14992* (A); Santa Cruz Mountains, near Hampton School, alt. 2400 ft., *Webster & Proctor 5293* (A, JAM). TRELAWNY: Ramgoat Cave, *Howard 14129* (A); Tyre, alt.

1750 ft., *Proctor 9936* (GH); road to Troy, *Harris 8687* (F, NY, US); Troy and vicinity, *Britton 929* (NY), *Perkins 1331* (GH, HOLOTYPE of var. *trojanus*). MANCHESTER: Brown's Town to Porus, hillside, *Britton 3272* (F, NY); vicinity of Mandeville, *S. Brown 248* (A, NY); 1.5 miles north of Shooters Hill, *Howard 14107* (A). ST. ANN: interior of St. Anns, *Purdie* (P, type collection of var. *purdiaena*); Guys Hill, Moneague, *Alexander* (G); Union Hill, near Moneague, *Britton & Hollick 2747* (F); Discovery Bay, *Hunnewell 18844* (GH). CLARENDON: Croft's Mountain, alt. 2500 ft., *Harris 11212* (F, NY). ST. CATHERINE: Old Harbour Bay, Little Goat Island, rocky woods, *Britton & Hollick 1855* (F, NY); Great Goat Island, southeastern side, *Harris 9301* (A, C, JAM, NY), *9337* (A, C, NY); Devil's Race Course, *Proctor 7213* (MICH). ST. ANDREW: valley of Yallahs River, *Alexander* (NY); Rock Fort, *Campbell 6412* (NY); near Hope, *Harris 8601* (JAM, NY), *8950* (JAM, NY, US); Hope River gorge, August Town, *Powell 297* (A). PORTLAND: Swift River gorge at Eden, *Proctor 11868* (GH); Uncommon Hill, *Proctor 8555* (GH); Port Antonio, Cave Hill near railway station, *Wight 199* (F, NY); John Crow Mountains, above Ecclesdown, rain-forest, *Howard, Proctor & Stearn 14769* (A). ST. THOMAS: Mansfield, *Britton 3557* (NY); Golden Valley, *Harris 5423* (F, NY); Plantain Garden River gorge, northwest of Whitehall, *Proctor 7419* (GH); Whitehall to Big Hill, *Proctor 7671* (JAM); Big Level, southeast end of John Crow Mountains, *Proctor 11820* (GH), *Webster & Proctor 5516* (A, BM, JAM, MICH, US).

Not only is *P. nutans* one of the most variable of the West Indian species, but its Jamaican representative (ssp. *nutans*) is certainly one of the most widespread woody plants on that island; it occurs from sea-level (at Rock Fort) to 2,500 ft. in the hills of the interior, and from such arid localities as Great Goat Island to dripping rain forest in the John Crow Mountains where the precipitation certainly exceeds 200 inches per year. The only sizeable area on the island where it appears to be absent is the upper slopes of the Blue Mountains (above 3,000 ft.); although it has most often been collected on limestone, it has also been found growing on serpentine (e.g., *Proctor 7419*).

In view of its ubiquitous distribution on Jamaica, it is not surprising that ssp. *nutans* should exhibit so much variability; but any attempt to categorize these variations can only encounter great difficulty. Even the distinction between the two subspecies is not very well-marked and may prove to be untenable when more collections are available from the Cayman Islands and Cuba. Since it has not proved very useful to express the intraspecific variation in terms of conventional taxa, a series of maps plotted for individual characters has been prepared. Many characters, of course, show a purely random distribution, as Map XIX shows for the presence or absence of pubescence. It is curious, however, that in the related species of this section, *P. barbadensis* and *P. botryanthus*, there is no variation in this respect, all individuals being hirsutulous and glabrous respectively. The distribution of reddish color in the calyx, plotted on Map XX, is a somewhat more doubtful case, for it might appear that there is a bicentric distribution of green calyces; however, the number of samples is small (due to the difficulty in ascertaining the color if there



MAPS XIX-XXI. Distribution of certain morphological characters in populations of *Phyllanthus nutans* Sw. The symbols separated by heavy lines in the upper left-hand and right-hand corners refer to the disjunct populations in the Cayman Islands and eastern Cuba, respectively. The numbers associated with the dots in Map XIX indicate the mean stylar length (in tenths of a millimeter) of the individual samples, while the numbers in Map XX refer to the mean seed length in tenths of a millimeter. All herbarium specimens from definite localities are plotted in Map XIX, but some of these do not appear in Maps XX and XXI because of incomplete data.

are no label data) and it seems likely that further collections may break down the apparent distinction.

There are, however, a number of characters which show undoubted geographically correlated variation and it might be thought that these could serve as the basis for the recognition of subspecies or varieties. For instance, it is quite evident that in seed size, length of stylar column, and inflorescence-type the plants from the western part of the island show differences from the eastern populations. But a closer inspection will show that although there is a *general* east-west separation (and this holds, on a larger scale, between Jamaica and Cuba), the characters vary independently of one another to such an extent that no satisfactory minor taxa can be defined within the Jamaican plants as a whole. Thus var. *trojanus*, which was previously defined on the basis of plants with a long stylar column, must be relegated to synonymy, for the plants from Dolphin Head which otherwise agree with the plants from Troy in their inflorescence and leaves have much shorter stylar columns. The var. *purdieanus* recognized by Baillon and Mueller is an even less significant variation (of conspicuously bracteate inflorescences) which has a purely random distribution.

The two most striking character differences within *P. nutans* certainly deal with the stipule and inflorescence types, and it is indeed upon this fact that the two subspecies are recognized. It must be admitted, however, that even here the correlation is far from perfect. The Cuban ssp. *grisebachianus* clearly differs from most forms of ssp. *nutans* in its solitary axillary flowers and persistent stipules; but some plants in western Jamaica have essentially axillary flowers, while in the Cayman Islands and in the John Crow Mountains at the eastern end of Jamaica occur some anomalous forms with persistent stipules but which in other respects are more or less typical for ssp. *nutans*. It is clear, in the case of the John Crow plants, that the persistent stipules have been derived independently of those in ssp. *grisebachianus*; and a collection from the central part of the John Crow range (*Howard & Proctor 14769*) is furthermore so divergent that it was at first thought to represent a distinct species. In this collection the leaves are conspicuously corrugated, quite unlike any other specimens of *P. nutans*, even though the difference becomes obscured in drying. However, the inflorescence is typical for ssp. *nutans*, and the persistent stipules are shared by a collection from the Big Level area of the John Crow Range (*Webster & Proctor 5516*) which seems otherwise to represent ssp. *nutans*. Thus, despite the importance of the morphological divergence in the John Crow Mountains population, it does not seem practicable to designate it as a species or even subspecies.

The plants from the Cayman Islands, although not showing any divergence as extreme as the bullate-leaved form from the John Crows, are of great interest in that they bridge rather nicely the gap between the two subspecies. The two collections from Grand Cayman seem assignable to ssp. *nutans* by virtue of their ovate leaves, but they are to some extent transitional, because *Proctor 15245* has the axillary flowers of ssp. *grisebachianus* combined with the deciduous stipules of ssp. *nutans*, while

Proctor 11977 has the thyrsoïd flowers of ssp. *nutans* combined with apparently persistent stipules as in ssp. *grisebachianus*. The collection from Little Cayman (*Kings LC42*), on the other hand, is clearly referable to ssp. *grisebachianus*, since it has elliptic, revolute leaves, persistent brownish stipules, and flowers axillary (or mostly so). While it is perhaps arbitrary to assign the Grand Cayman plants to ssp. *nutans*, there is in any event no doubt that the Cayman Islands population forms a connecting link between the two subspecies. Possibly the key to understanding the present distribution of *P. nutans* lies in the geological history of the Cayman Islands.

45b. *Phyllanthus nutans* ssp. *grisebachianus* (Muell. Arg.) stat. nov.
(PLATE XXIV, figs. G-H).

Phyllanthus grisebachianus Muell. Arg. *Linnaea* 32: 26. 1863; DC. *Prodr.* 15(2): 380. 1866.

Diasperus grisebachianus (Muell. Arg.) O. Ktze. *Rev. Gen. Pl.* 2: 599. 1891.

Stipules scarious, chartaceous, persistent (at least the basal portion), lanceolate, 2–3.5 mm. long, 0.7–1.5 mm. broad, truncate at the base, glabrous or hirsutulous, dark brown. Leaf-blades elliptic, glabrous or hirsutulous beneath, acute at tip and base, margins narrowly revolute. Flowers entirely axillary, solitary or the male and female paired at each axil. Calyx-lobes of male and female flowers denticulate, thin, the midrib conspicuously branched. Styler column c. 0.5–0.7 mm. high; style-ends reflexed, dilated, bifid or notched, the tips recurved. Seeds c. 4.5 mm. long.

TYPE: eastern Cuba, *Wright 582*.

DISTRIBUTION: eastern Cuba (Sagua-Baracoa range) and Cayman Islands (MAPS XVIII–XXI).

CAYMAN ISLANDS: Little Cayman, South Town, *Kings LC42* (BR, NY). CUBA. ORIENTE: "Cuba Orientali," *Wright 582* (G, HOLOTYPE; A, BR, G, GH, GOET, ISOTYPES); Monte Verde, 10 May 1859, *Wright 1436* ex. p. (BR, G, GH, S; mixed in some collections with *Margaritaria scandens*).

As here circumscribed, ssp. *grisebachianus* is readily distinguishable from ssp. *nutans* except in the Cayman Islands. The association of the *Kings* collection from Little Cayman with ssp. *grisebachianus* rather than with the Grand Cayman plants (which are assigned to ssp. *nutans*) is based on its pointed revolute leaves hirsutulous beneath (on the midrib) and its dark persistent stipules. However, it must be granted that the Little Cayman specimen shows several discrepancies as compared with the Cuban plants, for it has female pedicels 15–30 mm. long and female flowers which are neither all solitary nor all axillary to unreduced leaves, whereas the Cuban collections show pedicels 6–14 mm. long and have completely solitary, axillary flowers. The population on Little Cayman may, therefore, be classified as transitional between the two subspecies but with the stronger leaning to ssp. *grisebachianus*, whereas the Grand

Cayman plants fall closer to *ssp. nutans*. Additional collections, particularly from Cayman Brac and from Cuba, might provide a decisive test of the practicability of the present classification. It may prove to be unfeasible to maintain two subspecies if additional break-down in the characters is shown to exist; but, for the present, the Cuban and Jamaican populations appear to be sufficiently distinct from one another to warrant separation.

46. *Phyllanthus pachystylus* Urb. Symb. Ant. 3: 286. 1902.

(PLATE I, fig. 2; PLATE XXIV, figs. I-L).

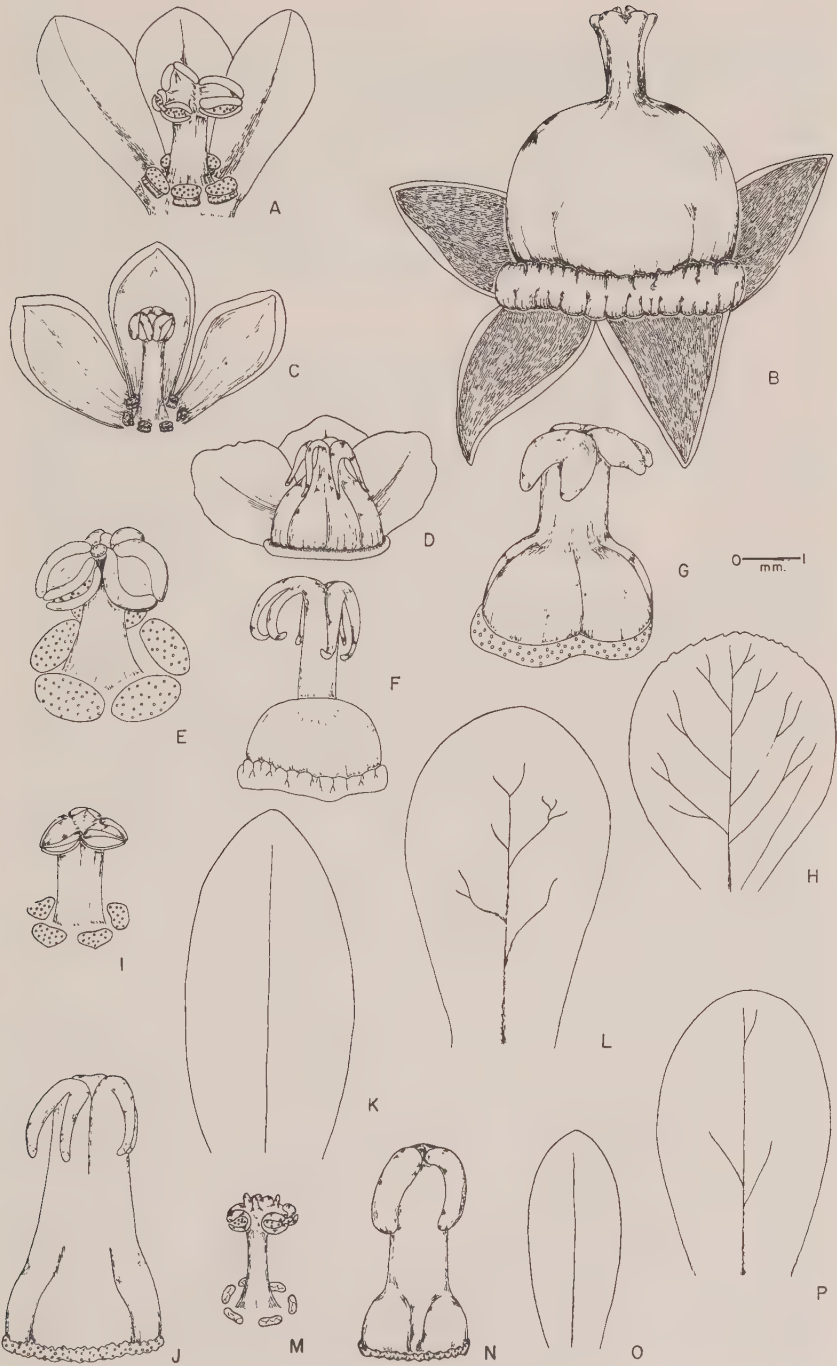
A slender sparsely branching shrub (usually with a single main stem) becoming 1–1.5 m. high; main stem 3–5 mm. thick, terete, bark burnished and reddish brown becoming greyish and fissured; branches mostly steeply ascending, reddish brown angled, furrowed, glabrous or rarely hirsutulous, becoming mostly 8–25 cm. long, c. 1.2–2.5 mm. thick, with c. 5–15 nodes. Leaves: stipules lanceolate to linear-lanceolate, (1.2–) 1.5–2 (–3) mm. long, 0.4–1 mm. broad, acute, glabrous, becoming darkened and indurate, persistent, entire. Petioles stout, glabrous or rarely hirsutulous, 2.5–5 mm. long. Leaf-blades becoming rigidly coriaceous, mostly elliptic-oblong (varying to narrowly elliptic, ovate, or lanceolate), mostly 3.5–7 (–9) cm. long, (1–) 1.5–3.5 (–4.5) cm. broad, obtuse, rounded, or retuse at the tip, acute to obtuse at the base; above dark purplish (drying blackish) when young, becoming more or less olivaceous-plumbeous, essentially smooth (often somewhat wrinkled), the midrib and lateral veins noticeably sunken; beneath much paler, alveolar-pruinose, the midrib prominently raised, the spreading to ascending laterals (5–7 on a side) somewhat raised, the reticulum of veinlets often visible; margins thickened, conspicuously revolute.

Monoecious; cymules mostly bisexual, each with 1–3 female and 2–10 male flowers, in the axils of bracts on naked pseudo-terminal thyrses (the thyrses produced from one or several axils immediately below the tip of the branchlet); cymules sometimes unisexual.

Male flower: pedicel capillary, smooth or rarely hirsutulous, 7–12 mm. long. Calyx-lobes 6, rather fleshy, biseriate (but sometimes obscurely so),

PLATE XXIV. FLOWERS OF SECT. *Elutanthos*.

FIGS. A–B. Male and female flowers of *Phyllanthus botryanthus* Muell. Arg. (*Haught 6556* [GH]). FIGS. C–D. Male and female flowers of *Phyllanthus anderssonii* Muell. Arg. (*Warming 27* [C]). FIGS. E–F. Androecium and gynoecium of *Phyllanthus nutans* Sw. *ssp. nutans* (*Proctor 15245* [GH], *Webster & Wilson 5075* [A]). FIGS. G–H. Gynoecium and female calyx-lobe of *Phyllanthus nutans* *ssp. grisebachianus* (Muell. Arg.) Webster (*Wright 1436* [S]). FIGS. I–L. Androecium, gynoecium, inner and outer female calyx lobes of *Phyllanthus pachystylus* Urb. (androecium, *Howard 6199* [GH]; others, *Ekman 15037* [S]). FIGS. M–P. Androecium, gynoecium, and inner female calyx-lobes of *Phyllanthus urbanianus* Mansf. (*Ekman H10435* [S]).



WEBSTER, WEST INDIAN PHYLLANTHUS

(2-) 2.3-3 mm. long, outer lobes usually oblong and obtuse, c. 1.3-1.6 mm. broad, with midrib simple or nearly so, inner lobes usually obovate, c. 1.5-2 mm. broad, with midrib usually sparsely branched (occasionally simple); lobes entire or sparsely denticulate. Disk-segments 6, usually rather massive, reniform to elliptic, foveolate, c. 0.3-0.6 mm. across. Stamens 3; column rather stout, (0.6-) 0.75-0.9 (-1) mm. high, mostly 0.4-0.6 mm. thick; anthers sessile atop the column, basally connate, the common connective plane or umbonate, triangular, c. 0.3-0.55 mm. long and 0.4-0.6 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21-24 μ in diameter, areoles polybrochate, c. 4-6 μ across.

Female flower: pedicel slender, terete, more or less reddish, glabrous or rarely hirsutulous, 2.5-6 (-8) mm. long, 0.3-0.5 mm. thick. Calyx-lobes 6, distinctly biseriate, (2-) 2.5-3.5 (-4) mm. long, entire or obscurely denticulate; outer lobes narrowly oblong with midrib almost or quite unbranched (rarely copiously pinnately branched), c. 1-1.5 (-1.9) mm. broad; inner lobes obovate or spatulate with midrib always pinnately branched, c. 1.4-2.2 mm. broad; lobes entire or obscurely denticulate. Disk shallowly cupuliform, angled, finely crenulate. Styles connate or coherent into a massive column (0.5-) 0.7-1 (-1.5) mm. high which is not sharply demarcated from the ovary; free ends of styles recurved, 0.4-0.6 (-0.9) mm. long, more or less dilated, parted $\frac{1}{2}$ to $\frac{3}{4}$ their length, the tips broadly triangular to lanceolate, obtuse to acute.

Capsule rounded in outline, c. 5 mm. high and 8 mm. broad, rarely remaining entire, the valves rugulose. Columella rather massive, (3-) 4 (-4.5) mm. high. Seeds trigonous, nearly symmetric, (4-) 4.5-5.4 mm. long, 2.7-3.1 mm. radially, 2.9-3.5 mm. tangentially, light brown, smooth (very finely striolate); hilum submedian; micropylar end sometimes developing a conspicuous whitish caruncle.

Collected in flower and fruit April through September.

TYPE: Cuba, Oriente, *Wright* 1947.

DISTRIBUTION: endemic to the Sagua-Baracoa massif, eastern Cuba (MAP XVIII).

CUBA. ORIENTE: Sierra de Nipe, near Río Piloto, *Ekman* 2274, 6028, 15037 (S); Charrascal de la Cueva, Mayarí, *León et al.* 19888 (MICH); wooded hillside, San José, *Howard* 6199 (GH, NY); near Woodfred, deciduous woods and thickets, *Shafer* 3617 (NY); edge of savannas near Sagua de Tánamo, 3 April 1861, *Wright* 1947 (GH, LECTOTYPE; G, GOET, ISOTYPES); pinars near Moa, *Acuña* 12503 (US), *Bucher* 102, 107 (NY), *Clemente* 3555 (MT), *Marie-Victorin et al.* 21565 (A, MT), 21705 (MT); Franklyn Mine, *Clemente & Alain* 3890 (MICH); Playa La Vaca, *Clemente* 4918 (MICH); Cerro de Miraflores, *Marie-Victorin et al.* 21557 (A, MT); dense pine woods 15 kms. southwest of Moa mill, *Howard* 5955 (GH); pinelands on serpentine between Río Moa and Río Yagrumaje, *Webster* 3757, 3771 (MICH); Cayo Chiquita, 8 km. south of Moa, *Webster* 3848 (GH, MICH); pine scrub 10 km. south of Moa, *Webster* 3895 (GH, MICH); scrublands 16 and 18 km. south of Moa, *Webster* 3906, 3907 (GH, MICH).

This species has a very characteristic appearance in the field due to its shiny, coriaceous, purplish leaves and nodding inflorescences which may even be twining in dense undergrowth. Unlike the other West Indian species of sect. *Elutanthos*, which are predominantly calciphiles, *P. pachystylus* appears to be confined to serpentine; and like many species in other genera growing on the limonite soils of the Moa region, it shows a greater degree of apparent morphological adaptation to dry conditions than do its related congeners. Ekman noted on his labels that in the Sierra de Nipe the species is rare and becoming extinct; but in the Moa area it is certainly still thriving and in fact is one of the commonest undershrubs in the open pinelands there.

The closest relationship to *P. pachystylus* appears to be shown by *P. nutans* ssp. *grisebachianus*, which occupies a clearly allopatric range in the Monte Verde area, although the gap in range may be no more than about 20 or 25 miles. The thinner stipules and leaf-blades, solitary axillary flowers, longer female pedicels, and less massive styles of that plant present so many distinctions that there can be no doubt as to the specific distinctness of *P. pachystylus*.

47. *Phyllanthus urbanianus* Mansf. Repert. Sp. Nov. 32: 86. 1933.
(PLATE XXIV, figs. M-P).

A small shrub (probably with the aspect of *P. pachystylus*); main stem subsimple, c. 2.5 mm. thick, terete, bark dark reddish brown, reddish hirsutulous; ultimate branches reddish brown, terete, somewhat furrowed, reddish hirsutulous, c. 20–35 cm. long, 0.9–1 mm. thick, with c. 20–45 nodes. Leaves: stipules narrowly lanceolate, 1.2–1.8 mm. long, 0.25–0.5 mm. broad, acute, thin and scarious, olivaceous becoming dark brown and persistent. Petioles rather slender, reddish- or hyaline-hirsutulous, c. 3–4 mm. long. Leaf-blades chartaceous, elliptic, c. 4–6.5 cm. long and 1.2–2.7 cm. broad on main stem, decreasing to 1.5–3 cm. long and 0.4–1.2 cm. broad at tips of branches, acute at the tip, acute to obtuse at the base; above dark olivaceous, reddish hirsutulous along the scarcely raised midrib and laterals; beneath pale, copiously hirsutulous throughout, the midrib and laterals (4 or 5 on a side) raised, light brownish; margins unthickened, narrowly revolute.

Monocious; cymules mostly bisexual, each with a single central female flower and several lateral males, in the axils of semi-reduced (still leaf-like) bracts on distal branches (which are homologous with the "naked" thyrses of *P. nutans*); individual cymules occasionally replaced by depauperate inflorescence axes.

Male flower: pedicel capillary, smooth to copiously hirsutulous, c. 8–10 mm. long. Calyx-lobes 6, c. 2.2–2.5 mm. long, more or less biseriate: outer lobes narrowly oblong, c. 0.75 mm. broad, inner lobes elliptic-oblong, slightly over 1 mm. broad; lobes all rounded at the tip, reddish with rather ill-defined yellowish margins, the midrib simple or sparingly branched. Disk-segments 6, flattened, roundish, foveolate, c. 0.2–0.3 mm. across.

Stamens 3; column c. 0.8 mm. high, slightly constricted above; anthers sessile, c. 0.25 mm. long and 0.4 mm. broad, alternating with three erect apiculae c. 0.2 mm. long; anther-sacs rather broadly divaricate, dehiscing horizontally; pollen grains 18–21 μ in diameter, areoles transitional between oligobrochate and polybrochate, c. 4–6 μ across.

Female flower: pedicel slender, terete or nearly so, sparsely to copiously hirsutulous, 12–15 mm. long. Calyx-lobes 6, biseriate: at anthesis, outer lobes linear-oblong, obtuse, with simple midrib, 2–2.3 mm. long and 0.8–0.9 mm. broad, inner lobes obovate, rounded at the tip, with sparingly branched midrib, 2.7–3 mm. long and 1.3–1.5 mm. broad; lobes chartaceous, reddish, essentially entire, becoming reflexed in fruit. Disk shallowly cupuliform, 6-angled, rather fleshy, crenulate. Styles connate into a massive column c. 1 mm. high and 0.5 mm. broad; free ends of styles recurved, dilated, oblong, obtuse or emarginate, c. 0.4–0.6 mm. long.

Capsule c. 4 mm. high and 7 mm. broad, somewhat rugulose. Columella c. 2.5 mm. high. Seeds trigonous, slightly asymmetric (somewhat umbonate at one corner), c. 4.2 mm. long, 2.7 mm. radially, 2.9–3 mm. tangentially, smooth, mottled light brown; hilum submedian.

TYPE: Haiti, Dept. Sud, Massif de la Hotte, western group, Les Roseaux, Hab. Gros-Roché, rocky forest, hard limestone, alt. 400 m., rare, 27 June 1928, *Ekman H-10435* (S, HOLOTYPE; A, US, ISOTYPES).

DISTRIBUTION: known only from the type collection (MAP XVIII).

This rare endemic species is of particular phytogeographic interest, because it is the only representative of the section on Hispaniola. It resembles both *P. pachystylus* and *P. nutans* (especially ssp. *grisebachianus*), but differs in its more hirsutulous parts and very distinctive staminal column and styles, so that there would appear to be no reason to question its specific distinctness. The Cuban and Jamaican affinities of *P. urbanianus* provide another good demonstration (in addition to species relationships in sects. *Cyclanthera* and *Hemiphyllanthus*) of the profound floristic division between the Sellean peninsula of Haiti and the remainder of Hispaniola.

Subgenus VIII. **Xylophylla** (L.) Pers. Syn. Pl. 591. 1807; emend.

Xylophylla L. Mant. 2: 147–148. 1771.

Trees or shrubs with phyllanthoid branching, the branchlets pinnatifid or bipinnatifid; monoecious or very rarely dioecious. Male flower; calyx-lobes 4–6; disk of as many segments, these free or united; stamens 2–15, free or more commonly united; anthers dehiscing vertically to horizontally; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6 (rarely 4); disk cupuliform or patelliform; ovary of 3 carpels; styles bifid or multifid, sometimes dilated at the tips. Fruit capsular; seeds 2 in each locule.

Included in this large, entirely American subgenus of about a dozen sections and 60 species are the majority of the neotropical woody species

of *Phyllanthus*. The West Indies are definitely the center of distribution and apparently also of the evolution of the group, but a few additional sections (e.g., *Oxalistylis* and *Ciccastrum*) are confined to South America. In Mueller's treatment in the "Prodromus" the sections and species here brought together were much scattered, the following of his sections belonging (at least in part) to subg. *Xylophylla*: 12, 16-19, 34 (in small part), 35-36, and 44. Persoon's original conception of subg. *Xylophylla* as including only the phylloclade-bearing species was of course much narrower than that here adopted, and in fact corresponds to sect. *Xylophylla* alone.

Because of the dominant position of representatives of subg. *Xylophylla* in the West Indies, its relationships are of particular interest. However, although certain lines of affinity are very apparent within the group, there are several unresolved problems which make impossible an accurate tracing of phylogeny. It is certain that there is a close relationship between subg. *Xylophylla* and subg. *Botryanthus*, and the approach is nearest between sects. *Asterandra* and *Elutanthos*, respectively. Some of the Central American species of sect. *Elutanthos* (e.g., *P. grandifolius*) resemble sect. *Asterandra* so clearly that there can be little doubt of a significant kinship. However, there are some obstacles, to be discussed more fully farther on, which make it at least uncertain that subg. *Xylophylla* can be directly derived from subg. *Botryanthus* via sect. *Asterandra*. The small number of stamens in the flowers of *Botryanthus* and the large capsule of such species as *P. grandifolius* are features which appear to be derivative; so that it is possible to read the evolutionary series the other way around and to postulate that subg. *Botryanthus* has been derived from sect. *Asterandra* by reduction in the androecium accompanied by loss of phyllanthoid branching and increase in fruit size.

Within subg. *Xylophylla* two main phyla can be discerned: a series beginning with sect. *Williamia* and running through sects. *Thamnocharis* and *Orbicularia*; and a series proceeding from sect. *Asterandra* to sects. *Epistylum*, *Hemiphyllanthus*, and *Xylophylla*. Standing alone is sect. *Omphacodes*, which is aberrant in many respects and which in fact resembles sect. *Ciccopsis* of subg. *Cicca* more than it does any single section of subg. *Xylophylla*. It is classified here because of its areolate pollen grains, but without strong conviction, and its relationships need to be further investigated.

The initial dichotomy between sect. *Williamia* and sect. *Asterandra* has some puzzling aspects which cannot yet be resolved. That the higher stamen number in *Williamia* may be a primitive character is attested by the clearly documented reduction-series to a lower number in the derived sections; furthermore, the seeds of *Williamia* are less highly modified than those of *Asterandra*. However, the South American sect. *Oxalistylis*, which is closely related to *Asterandra*, has more unspecialized seeds, and perhaps can be thought of as a group more or less coördinate with *Williamia*, if indeed the two are not descended from some immediate common ancestor.

The anatomical evidence from leaves, as shown earlier in this study

(Jour. Arnold Arb. 37: 220. 1956), demonstrates for many taxa of this subgenus an interesting correlation between floral modification and increasing sclerification of foliar tissue. The rationale for this would appear to be that the evolutionary history of many of the groups of subg. *Xylophylla* has been one of increasing adaptation to xeric conditions. However, the adaptive radiation has been rather complex, so that no over-all generalizations on the ecology of the species can be made. In both the *Williamia* and *Asterandra* lines, however, the end-products of evolution (viz., sects. *Orbicularia* and *Xylophylla*) comprise species so altered in appearance that their ancestry could scarcely be guessed if it were not possible to trace it back through intervening species.

KEY TO THE SECTIONS

1. Branchlets pinnatifid.
 2. Styles each terminating in a dilated more or less crenate to lacerate stigma.
 3. Disk-segments of male flower free or at least not completely united; seeds thin-walled, neither fissured nor mottled; petioles without undulate marginal ridges.
 4. Leaves obtuse or emarginate at the tip; styles not calyptriform or if so then branchlet leaves opposite; stamens 3–15. . . . 16. *Williamia*
 4. Leaves acuminate; styles calyptriform or united into a massive column; stamens 2 or 3 (rarely 4); at least some inflorescences cauliflorous (except in *P. axillaris*). 21. *Epistylum*
 3. Disk-segments of male flower connate into a massive ring.
 4. Leaves acuminate, neither revolute nor golden beneath, the petiole with conspicuous undulate-ruffled margins; seeds thick-walled, mottled (as in *Ricinus*); stamens 3–5. 20. *Asterandra*
 4. Leaves blunt at the tip, revolute, golden beneath, the petiole without ruffled margins; seeds thin-walled, blackened and fissured; stamens 2. 22. *Glyptothamnus*¹⁹
 2. Styles bifid, the branches usually slender, never lacerate (rarely adaxially auriculate).
 3. Capsule somewhat fleshy, tardily dehiscent; leaf-blades chartaceous, the blade decurrent on the petiole; stamens 3. 19. *Omphacodes*
 3. Capsule dry, promptly dehiscent; leaf-blades chartaceous to coriaceous, the blade not decurrent on the petiole; stamens 2–6.
 4. Leaf-blades small (less than 2 cm. long), with conspicuous mesophyllar sclereids, often concave beneath and with revolute margins; seeds less than 3 mm. long; stipules more or less persistent; flowers mostly appearing after the leaves. 18. *Orbicularia*

¹⁹ Sect. *Glyptothamnus*, sect. nov. Frutices monoicae, foliis coriaceis revolutis subtus aureis; cymulis unisexualibus; flore masculo laciniis calycis 4, disco integro summopere dilatato, staminibus 2 filamentis connatis, antheris horizontaliter dehiscentibus, granis pollinis globosis areolatis; flore femineo laciniis calycis 5, disco magno integro, stylis dilatatis laceratis; seminibus fuscis sulcatis. — Species typica *Phyllanthus chryseus* Howard (sectional epithet from Gr. *glyptos*, carved, and *thamnus*, shrub, in allusion to the appearance of the massive flowers and leaves).

4. Leaf-blades larger, the sclereids aggregated within the plane, thickened marginal rim (rather than in the mesophyll); seeds over 3 mm. long; stipules caducous; flowers appearing with the leaves. 17. *Thamnocharis*
1. Branchlets bipinnatifid, or modified into phylloclades.
2. Branchlets not greatly dilated, bearing typical leaves, the penultimate axis incrustate or scurfy. 23. *Hemiphyllanthus*
2. Branchlets dilated and transformed into phylloclades, the leaves normally absent except on seedlings; axes never incrustate or scurfy. 24. *Xylophylla*

Sect. 16. *Williamia* (Baill.) Muell. Arg. *Linnaea* 32: 4. 1863; DC. *Prodr.* 15(2): 328. 1866.

Williamia Baill. *Etud. Gen. Euphorb.* 559, *pl.* 27, *figs.* 9-10. 1858.

Shrubs with phyllanthoid branching; leaves chartaceous to coriaceous, stipules deciduous or persistent. Monoecious, cymules bisexual, the flowers maturing after the leaves. Male flower: calyx-lobes 5 or 6; stamens 3-15 (very rarely 2), filaments united into a column, anthers in 1-3 whorls; pollen grains areolate. Female flower: calyx-lobes 5 or 6; disk plane, angular, often massive; ovary sessile or definitely stipitate; styles erect or spreading, free or connate, the distal ends dilated and lacerate or dentate. Capsule oblate, dry, not veiny; seeds colliculose or verruculose, less than 3 mm. long.

TYPE SPECIES: *Williamia pruinosa* Baill. (= *Phyllanthus discolor* Poepp. ex Spr.).

As here defined, the circumscription of sect. *Williamia* is enlarged from that previously held (*Contr. Gray Herb.* 176: 57. 1955; *Jour. Arnold Arb.* 37: 220. 1956) by the inclusion within it of sect. *Williamiandra*. The emended section thus comprises seven Cuban species which are indubitably related, although they are morphologically so far divergent from one another that the group might at first sight appear to be an unnatural one. A well-marked evolutionary series of increasing specialization may be traced between *P. discolor*, with its thin, unsclerified leaves and androecium of up to 15 stamens, and *P. incrustatus*, which has highly sclerified leaves and only 2-4 stamens. However, despite the prominence of these phylogenetic trends, the relationships of the species of the three subsections cannot be visualized as a simple and clear-cut "family tree."

The affinity of sect. *Williamia* with sects. *Orbicularia* and *Thamnocharis* is particularly clear in view of the fact that the latter appear to be its direct offspring. In fact, the ancestry of both sections may with reasonable confidence be traced back to subsect. *Discolores*, since *Orbicularia* and *Thamnocharis* would appear to have been derived from progenitors similar to *P. microdictyus* and *P. discolor*, respectively. In both instances differentiation of the derived taxa has involved increased foliar sclerification, but this has occurred in a strikingly different manner, for the sclereids are scattered through the mesophyll in sect. *Orbicularia*, whereas they are

aggregated within the marginal rim of the lamina in sect. *Thamnocharis*.

Because of its ancestral relationship to sects. *Orbicularia* and *Thamnocharis*, as well as the relatively unspecialized morphological features of its subsection *Discolores*, sect. *Williamia* has been placed first in the linear arrangement of sections under subg. *Xylophylla*. However, this is not intended necessarily to imply that *Williamia* is the most primitive of all the taxa within the subgenus. The differences in stamen number on which Mueller laid such stress appear far less significant in the light of present knowledge, for the stamen number of *P. discolor* is mostly 10-13 instead of the 15 reported in the literature; and in any event, even the former number is by no means a certain indication of primitiveness. The sister species of *P. discolor*, *P. microdictyus*, is more similar in floral characters to the South American sect. *Oxalistylis*. It appears that *P. discolor* and *P. microdictyus* may best be regarded as vicarious descendants from a common ancestor, specialization having progressed further in the flowers of the former and the leaves of the latter.

The flowers of *P. salviaefolius*, the type (and only?) species of sect. *Oxalistylis*, are so similar to those of *P. microdictyus*, particularly with regard to the gynoeceum, that the possibility of uniting sects. *Oxalistylis* and *Williamia* might possibly be considered. However, the South American species differs by having several female flowers per cymule, differently ornamented seeds, and very different leaves much more like those of sect. *Asterandra*; so, for the time being, it seems justifiable to maintain the two sections as distinct.

KEY TO THE SUBSECTIONS AND SPECIES

1. Leaves of branchlets alternate; stigmas (style-tips) not calyptriform.
 2. Stems smooth, lenticels (if present) sparse and inconspicuous; stamens 6-15. Subsect. 16a. **Discolores**
 3. Leaves chartaceous, not highly sclerified.
 4. Calyx-lobes of female flower 2-3 mm. long; styles less than 2 mm. long; stamens mostly 9-13; leaf-blades irregularly reticulate above. 48. *P. discolor*
 4. Calyx-lobes of female flower 7-8.5 mm. long; styles 3.5-5 mm. long; stamens 6-10; leaf-blades finely and evenly reticulate above, the areoles straight-sided. 49. *P. microdictyus*
 3. Leaves coriaceous, with abundant mesophyllar sclereids. 50. *P. cristalensis*
2. Stems incrustate, the bark breaking up into small platelets separated by spongy tissue; stamens (2-) 3-6. Subsect. 16b. **Incrustati**
 3. Stipules of branchlets acicular-conduplicate, mostly caducous; staminal column prolonged into a terminal apiculum; disk of female flower with a crenate upturned rim; leaves mostly 1.5-2.5 cm. long. 51. *P. williamiioides*
 3. Stipules of branchlets nearly plane, indurate and persistent; staminal column not apiculate; disk of female flower plane, entire.
 4. Leaf-blades 2.5-4.5 cm. long, prominently reticulate beneath;

- pedicel of female flower 10–15 mm. long; stamens 5 or 6. 52. *P. excisus*
4. Leaf-blades 0.7–1.5 cm. long, obscurely reticulate beneath; pedicel of female flower 1–3 mm. long; stamens 3 or 4 (rarely 2). 53. *P. incrustatus*
1. Leaves of branchlets opposite; stigmas (dilated style-tips) forming a cap covering most of the ovary; axes with conspicuous lenticels. Subsect. 16c. *Mirifici*
- Only species 54. *P. mirificus*

Subsect. 16a. *Discolores*, subsect. nov.

Williamia Baill. Etud. Gen. Euphorb. 559, pl. 27, figs. 9–10. 1858.

Phyllanthus sect. *Williamia* (Baill.) Muell. Arg. in DC. Prodr. 15(2): 328. 1866 (ex p.).

Stems smooth, lenticels obsolete or sparse; leaves of branchlets alternate, chartaceous or (in *P. cristalensis*) coriaceous and sclerified; stamens 6–15 (number unknown in *P. cristalensis*); styles erect, the tips moderately dilated.

TYPE SPECIES: *Phyllanthus discolor* Poepp. ex Spr.

There can be no doubt that subsect. *Discolores* occupies a significant position in the evolutionary sense, for sects. *Thamnocharis* and *Orbicularia* may with a high degree of probability be spoken of as derived from *P. discolor* and *P. microdictyus*, respectively. If, as suggested above, the high stamen number of *P. discolor* is secondarily derived from a 5- or 6-merous condition, there has at any rate been a reduction in number in the species of the derived taxa (subsect. *Incrustati*, sects. *Thamnocharis* and *Orbicularia*).

The inclusion of *P. cristalensis* within this subsection can only be provisional, for its floral characters are still insufficiently known. On the basis of its vegetative characters, it would appear to be related to *P. microdictyus* and *P. excisus*, since it has the smooth axes of the former and the highly sclerified leaves of the latter. Should its present position appear justified after the examination of adequate fertile material, *P. cristalensis* would represent a nearly schematic connecting link between subsections. *Discolores* and *Incrustati*.

48. *Phyllanthus discolor* Poepp. ex Spr. Syst. 3: 21. 1826.

(PLATE XXV, figs. A–C).

Phyllanthus pruinus Poepp. ex Rich. in Sagra, Hist. Nat. Cuba 11: 216. 1850; non sensu Muell. Arg. in DC. Prodr. 15(2): 387. 1866.

Williamia pruinosa (Poepp.) Baill. Etud. Gen. Euphorb. 560, pl. 27, figs. 9–10. 1858.

Diasperus discolor ("Spr.") O. Ktze. Rev. Gen. 2: 599. 1891.

Diasperus pruinus ("Rich.") O. Ktze. op. cit. 600.

Phyllanthus decander Sessé & Moc. Fl. Mex. ed. 2, 212–213. 1894.

A shrub becoming c. 1–2 m. high, sparsely branching, the main stem(s)

slender (mostly 2–3 mm. thick), light brown, smooth, terete, with brown pith. Cataphylls not indurate, early deciduous: stipules triangular to lanceolate, acute or acuminate, 4–8 mm. long and 1–2 mm. broad (smaller on weak shoots), truncate at the base, thin and scarious, dark reddish brown with narrow paler denticulate or entire margins; blade linear-lanceolate, acuminate, 4–6 mm. long and 0.7–1 mm. broad. Deciduous branchlets 8–15 (–25) cm. long, 0.7–1.3 mm. thick, light brown or stramineous, terete to distinctly flattened, with (5–) 7–14 (–16) leaves; first internode 1.5–3 cm. long, median internodes mostly 1–2 cm. long. Leaves: stipules thin and scarious, early deciduous (except at tips of branchlets), linear-lanceolate, acuminate, (2.5–) 3.5–6.5 (–7) mm. long, (0.4–) 0.7–1.2 mm. broad, brownish, with entire margins. Petioles 2–4 mm. long, subterete, dark brownish, smooth. Leaf-blades chartaceous, mostly ovate or elliptic, (2–) 2.5–4 (–5.5) cm. long, (1–) 1.3–3 (–3.5) cm. broad, narrowed to an obtuse (less commonly rounded or emarginate) inconspicuously apiculate tip, acute to truncate or rarely subcordate at the base; above olivaceous or bright green, the midrib and the arching, crooked laterals slightly raised; beneath whitish- or creamy-pruinose (due to a waxy coating), the midrib salient, the laterals (c. 5–7 on a side) raised, minor veinlets forming a fine reticulum; margins unthickened, plane or casually revolute.

Monoecious; branchlets usually but not always floriferous; cymules bisexual, each most often with 1 or 2 (3) central female and c. 4–6 lateral male flowers; bracteoles of cymules triangular, dark brown, scarious, persistent.

Male flower: pedicel (1.5–) 2–6 mm. long. Calyx-lobes 5, chartaceous, subequal or usually unequal, rounded at the tip, entire or minutely denticulate near the apex; outer lobes ovate or oblong, 1.2–2.5 mm. long and 0.9–1.3 mm. broad; inner lobes obovate or spatulate, 1.7–3.5 mm. long and 1.3–1.9 mm. broad, 3- to 5-nerved from the base. Disk-segments 5, roundish, smooth and entire, c. 0.3–0.5 mm. broad. Stamens (7–) 9–13 (–15); filaments connate into a column c. 1–2 mm. high, the free portions 0.2–0.75 mm. long, erect or arching and spreading; stamens spirally arranged or in two superposed whorls with a whorl of 3 (–5) terminating the column; anthers c. 0.2–0.4 mm. long, 0.25–0.5 mm. broad, the upper erect or ascending, the lower often spreading or deflexed; anther-sacs slightly divergent, dehiscing longitudinally, the slits contiguous but usually not confluent; pollen grains 18–27 μ in diameter.

Female flower: pedicel slender, becoming (3–) 5–13 (–17) mm. long. Calyx-lobes 5, distinctly unequal, rounded at the tip, entire, with several veins from the base (at least in the larger); outer lobes ovate or oblong, 1.2–1.8 mm. long, 0.6–1.3 mm. broad; inner lobes (2–) 2.5–3 mm. long, 1.5–2.8 mm. broad. Disk rather massive, obtusely 5-angled, foveolate, the margins plane and entire. Ovary oblate or foveolate, with 3 low but distinct ribs, usually sessile; styles erect, somewhat unequal, free or connate at the base, c. 0.3–0.7 mm. long, the dilated ends (stigmas) roundish or crescent-shaped, crenulate or lacerate (but often appearing entire due

to recurved tips of lobes), sometimes adaxially auriculate, 0.5–0.8 mm. broad.

Capsule oblate, smooth or somewhat rugulose, rounded in outline, reddish brown, c. 2.1–2.3 mm. in diameter. Columella slender, 1.2–1.5 mm. long. Seeds acutely trigonous, symmetric, 1.7–1.8 mm. long, 1.1–1.3 mm. radially, 1.2–1.25 mm. tangentially, brown with somewhat irregular longitudinal lines of transversely elongate dark reddish brown dots; hilum triangular, c. 0.4 mm. long.

Collected in flower and fruit January through August.

TYPE: "Ad rivulos Cubae in Sumidero," *Poeppig* (W, LECTOTYPE; BR, F, ISOTYPES). *Poeppig*'s material appears to include more than one collection. The lectotype collection is the one associated with the printed label reading "*Phyllanthus discolor* En pl. Cub. MSS. . ."; but several additional collections made in Cuba in 1823 by *Poeppig* (all apparently in Matanzas province) are preserved in the Vienna herbarium. A specimen in the Paris Museum bearing the label "*Phyllanthus pruinus* Poepp. (ad Spreng. ad Phyll. polygonoid. Nutt. ductus) Cuba. Sylvae lucidae" and a specimen collected for Sagra (also in the Paris Museum) represent the type material of *P. pruinus* Poepp. ex Rich.

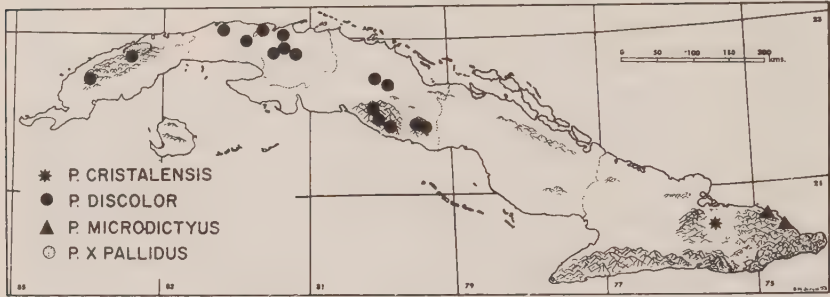
Although applied by Mueller and others to the plant known in this work as *P. caroliniensis* ssp. *saxicola*, the name *P. pruinus* Poepp. ex Rich. is actually a synonym of *P. discolor*. Its publication was apparently inadvertent, for *Poeppig*'s specific name, when it appears on the labels in script specially printed for his collection, is usually associated with specimens of *P. caroliniensis* ssp. *saxicola*. Evidently there was a mixture of labels in the case of the *Poeppig* specimens which went to Paris, so that Richard was misled into describing the present plant under a different name than that intended by *Poeppig*. Mueller (*Linnaea* 32: 30. 1863) independently published *P. pruinus* for the other plant, as designated by *Poeppig*, but this name must of course be rejected as a later homonym.

DISTRIBUTION: serpentine barrens and hillsides, central and western Cuba (MAP XXII).

CUBA: without locality, Sagra (A,P,W: SYNTYPES of *P. pruinus*). PINAR DEL RIO: Sumidero, between Hoyo Colorado and Francisco, at a brook, *Ekman* 18205 (S); Los Organos, Sabanilla, *Wright* 1941 ex p. (F, GH, GOET, MO, NY, P, S, US; data ex GH); pinelands, Loma Cajalbana, La Palma, *Alain* 2362 (GH); Sagua, Bahía Honda, *Wright* 1949 (G, GH, GOET; data ex GH); Rangel, Zambumbia Hill, *León* 12775 (MICH, NY). HABANA: La havane, 1821, *Leman* (P); Guanabacoa [ex Flor. Mex. ed. 2], *Sessé & Mocino* 4566 (F, TYPE COLLECTION of *P. decander*); eruptive rock soil, Madruga, *Britton, Britton, & Shafer* 631, 690 (NY), *León* 3330 (MT, NY). MATANZAS: cuabales northwest of Pan de Matanzas, southeast of Canasí, *Ekman* 16469 (S); savanna, Sabanilla de la Palma, *León, Roca, & Edmund* 9652 (NY); Tetas de Camarioca, serpentine barren; *Britton, Britton, & Wilson* 14063 (NY); Sumidero, *Poeppig* (W, LECTOTYPE; BR, F, MO, ISOTYPES)²⁰; San Miguel de los Baños, *Killip* 13867 (US),

²⁰ This collection is also a syntype collection of *P. pruinus*.

León & Roca 8907 (NY). LAS VILLAS: Palm barren, Santa Clara, *Britton & Cowell 10202* (NY); arroyo Ciento Viejo, 12.5 km. east of Santa Clara. *Howard 5081* (GH, MT), *Webster et al. 250* (GH); Trinidad Mountains, El Cumbre, thickets at a brook, *Ekman 13949* (S); near Pico Potrerillo, road to Aguada del Santo, open hillsides, quite common, *Ekman 13977* (S); Sierra de San Juan, Mina Carlota (southeast of Cumanayagua), alt. 300–400 m., *Howard 5663* (GH, MT, NY); Buenos Aires, *Roig & Acuña 6152* (NY); Loma de Tibisial, Sancti-



MAP XXII. Distribution of sect. *Williamia* subsect. *Discolores* in Cuba.

Spiritus Mountains, *León & Clement 6662* (NY); Lomas de Banao, *Luna 754* (NY); Lomas del Banao, Loma del Obispo, *Ekman 16282* (S), *León 1300* (NY).

Among the woody species of *Phyllanthus* in western Cuba, *P. discolor* is second only to *P. orbicularis* in abundance and frequency. As a consequence of the restriction of *P. discolor* to areas of serpentine outcrops, it occurs as a number of more or less isolated populations which exhibit a noticeable variation in leaf shape and stamen number. However, the variation within individuals is so high and the sampling of populations so inadequate (despite the rather considerable number of specimens examined) that the extent of geographical variation is difficult to assess. This inexact knowledge of the normal range of variation within the species presents a distinct hindrance in the analysis of some highly anomalous specimens from northern Pinar del Río.

These discordant collections, which all come from the Cajalbana region between La Palma and Bahía Honda, represent the plant to which the name *P. pallidus* has been applied. Grisebach (Goett. Nachr. 1865: 168.) differentiated *P. pallidus* from *P. discolor* on the basis of its glaucous, thicker leaves and greater crowding of anthers on the staminal column, while Mueller (DC. Prodr. 15 [2]: 328. 1866) proposed to distinguish it by its fewer flowers, the female with equal calyx-lobes and shorter pedicels, and by the pale leaves with indistinct venation. However, even a superficial survey of the specimens at hand is sufficient to show that none of these characters is stable or diagnostic. Consequently, the Cajalbana population was recently (Contr. Gray Herb. 176: 57. 1955) reduced to varietal rank under *P. discolor*; but even this disposition scarcely ap-

peared satisfactory in view of the extreme fluctuation of characters and the lack of geographical separation between the two entities.

An intensive study of a population sample taken between La Mulata and San Juan de Sagua, together with a reexamination of available herbarium specimens of *P. pallidus*, has led to the following interpretation of the situation.

Phyllanthus × *pallidus* Wr. ex Griseb. Goett. Nachr. 1865: 168. 1865, pro sp.
(= *P. discolor* × *P. comptus*.)

Phyllanthus sagraeanus Urb. Symb. Ant. 9: 182. 1924.

Phyllanthus discolor var. *pallidus* (Wr. ex Griseb.) Webster, Contr. Gray Herb. 176: 57. 1955.

CUBA. PINAR DEL RÍO: Cajálbana, Bahía Honda. *Wright 1950* (GOET. HOLOTYPE of *P. pallidus*; G, GH, ISOTYPES); Loma de Cajálbana, cuabales. *Ekman 10471* (NY, S; TYPE COLLECTION of *P. sagraeanus*); dense cuabales, eastern slope of Loma Cajálbana, *Ekman 17347* (S); orillas del arroyo, cerca de la cumbre de la Cajálbana, *León & Charles 4956* ex p. (NY); San José de Sagua to San Marcos, on serpentine rock, *Shafer 11971* (F, MO, NY, US); between La Mulata and San José de Sagua, *Webster 4652, 4653, 4654, 4657* (undistributed); Bahía Honda, dry rocky hillside, *Wilson 9417* (NY); locality questionable. *Wright 1941* ex p. (NY, P, S, US).

Some of the specimens cited have been annotated by formula rather than by the hybrid name, since they resemble *P. discolor* rather strongly and show only a subordinate influence of *P. comptus*. The type collection of *P. sagraeanus* is the most nearly intermediate, and *Wright 1950* (the type of *P. pallidus*) approaches this condition. The most striking vegetative difference between the two hybridizing species, the type of cataphyll (much more massive in *P. comptus*), is obscured in most specimens by the prevalence of *discolor* characteristics. Several collections, notably *León & Charles 4956* and *Wright 1941*, contain a mixture of *P. pallidus* and a form indistinguishable from typical *P. discolor*; in other collections there are intermediates of varying degrees.

The decision to regard the plants assigned to *P. pallidus* as hybrids between *P. discolor* and *P. comptus* has been taken after an extended analysis involving comparisons of leaf anatomy, pollen and seed fertility, and gross morphology. Anatomical studies of cleared leaves indicate that in *P. pallidus* the veinlets are c. 20–40 μ in diameter and are quite intermediate between the tenuous veinlets of *P. discolor* (mostly 10–20 μ thick) and the knobby ones of *P. comptus* (mostly 30–60 μ thick). Of even greater interest, although not entirely conclusive, are the results of a study of pollen grains taken from herbarium specimens and stained in lacto-phenol with cotton blue, which show that there is pollen sterility (though to a highly variable degree) in specimens which are transitional between *P. discolor* and *P. pallidus*, and essentially complete sterility in specimens which are morphologically good *P. pallidus*.

Since the assignment of specimens to *P. pallidus* or to the "transitional" column is somewhat arbitrary, Table II does not make sufficiently explicit

TABLE II†

POLLEN AND SEED FERTILITY

		Transitional between <i>P. discolor</i> and <i>P. pallidus</i>	
<i>P. discolor</i>		<i>Ekman</i> 17347	99
<i>Alain</i> 2362	94	<i>Shafer</i> 11971	99
<i>Ekman</i> 13977	99 (+)	<i>Webster</i> 4652-1	83 (-)
<i>Ekman</i> 16469	10, 46	4652-2	99 (-)
<i>Howard</i> 5081	72 (+)	4652-3	91
<i>Howard</i> 5563	96 (+)	4652-4	92
<i>Webster</i> 250	99 (+)	4652-5	20
<i>P. pallidus</i>		4652-6	14
<i>Ekman</i> 10471	— (*)	4652-7	70
<i>Webster</i> 4653-1	— (-, *)	4652-8	97
4654	64, 93 (-, *)	4652-9	100
4657	28, 40 (-)	4652-10	67
		4652-11	98
		4652-12	61 (-)
		4653-2	86
		4653-3	* (*)

† The figures following each collection number refer to the percentage of good pollen grains as determined by examination of 200 grains from each collection; in a few cases a second determination has been made from a different flower on the same plant. Only deeply stained grains of normal appearance have been counted as good; in doubtful instances they have been scored as defective. The plus and minus signs in parentheses refer to the production of seeds, any collection with fewer than 50% viable seed having been scored minus; lack of either symbol indicates that the degree of fertility could not be ascertained from the specimen. The asterisk denotes the production of monstrous flowers.

the important fact that the most nearly "typical" specimens of *P. pallidus* (i.e., ones such as *Ekman* 10471 which are exactly intermediate between *P. discolor* and *P. comptus*) are completely sterile, only the monstrous rudiments of female flowers being produced. Other collections, exemplified by *Webster* 4654 and 4657, definitely lean toward *P. pallidus* but have more or less normal flowers which are partially fertile. In the transitional plants trending toward *P. discolor* the fertility is as variable as the morphological features. *Webster* 4653-3 epitomizes the situation; it has vegetative features approaching typical *P. discolor*, but its completely monstrous flowers betray its reproductive instability.

The absence of collections intermediate between *P. pallidus* and the other presumed parent species *P. comptus* may appear strange, but is perhaps explained (at least in part) by the apparent rarity of the latter, which has been collected only three times. However, if this explanation is correct it raises the even knottier problem of why the hybrid form should be so much commoner than one of its parents, particularly since it appears to become fertile only when back-crossed to *P. discolor*. Possibly some ecological factor plays an important role in determining the peculiar character of the population.

The prevalence of "pallidus" characters in the Cajalbana population of *P. discolor* might be adduced as an instance of "introgressive hybridization," although it is not evident that any characters of *P. comptus* have been diffused into any populations of *P. discolor* outside of the Cajalbana area. Much more striking than any leakage of characters is the exaggerated variability of the local population as a whole; a considerable number of specimens show anomalous characteristics. An outstanding example of this is *Ekman 10433*, which vegetatively can scarcely be distinguished from typical *P. discolor* and which has highly fertile pollen; but its flowers are exceptional in the long staminal column and styles and the stipitate ovary. These peculiarities, especially the stipitate ovary, suggest a resemblance to the related species *P. microdictyus*, which is known only from Oriente province. However, it appears probable that these unusual features have some connection with the local hybridity and do not really signify any relationship to the species of Oriente.

The enhanced degree of variability is particularly marked in the stamen number, as shown in Table III. Since *P. comptus* usually has only 5 or 6 stamens, one would expect that its hybrids with *P. discolor* might have a number approaching the usual 9–13 of the latter. Insofar as the lower numbers (under 10) are concerned, this is reasonably well borne out. But the occurrence in *P. pallidus* of numbers much higher than those in *P. discolor* is entirely unexpected. Although the number of androecia counted (50 each of *P. discolor* and *P. pallidus*) is unfortunately small, there can be little doubt that mere chance cannot account for 11 of the *pallidus* flowers having a higher number than any of the *discolor* ones.

It seems quite likely that this wholly anomalous increase in stamen number in *P. pallidus* is the result of the same cause which determined the formation of a stipitate ovary in *Ekman 10433*, i.e., the morphogenetic disturbance in the hybrid plant which is presumably due to imbalance between the chromosome complements of the parents. It is conceivable that the situation in *P. pallidus* presents us with an insight into one mechanism of phylogenetic change, for if aberrant plants of *P. pallidus* with androecia of 16–18 anthers should happen to be selected out as a separate fertile population, a new species characterized by higher stamen number might result. Possibly the prevalent numbers (9–13) in *P. discolor* arose in this same way, for the primitive number in the genus is certainly 5 or 6 as in subg. *Kirganelia*; and since *P. discolor* has no other particularly primitive characters, it is probable that its increased stamen number, too, is derived.

The relationships of *P. discolor* are reasonably well-defined, for on purely morphological grounds its affinity to the following species, *P. microdictyus*, is apparent; and the general resemblance (though much less close) to *P. comptus* supports the evidence (from the existence of *P. pallidus*) that *P. discolor* can cross with that species. Furthermore, *P. comptus* in its morphological details is transitional between *P. discolor* and the other species of sect. *Thamnocharis*, so that it presumably has evolved from *P. discolor* or some common ancestor. The hybridization occurring today

TABLE III *

VARIATION IN STAMEN NUMBER IN
P. discolor AND *P. pallidus*

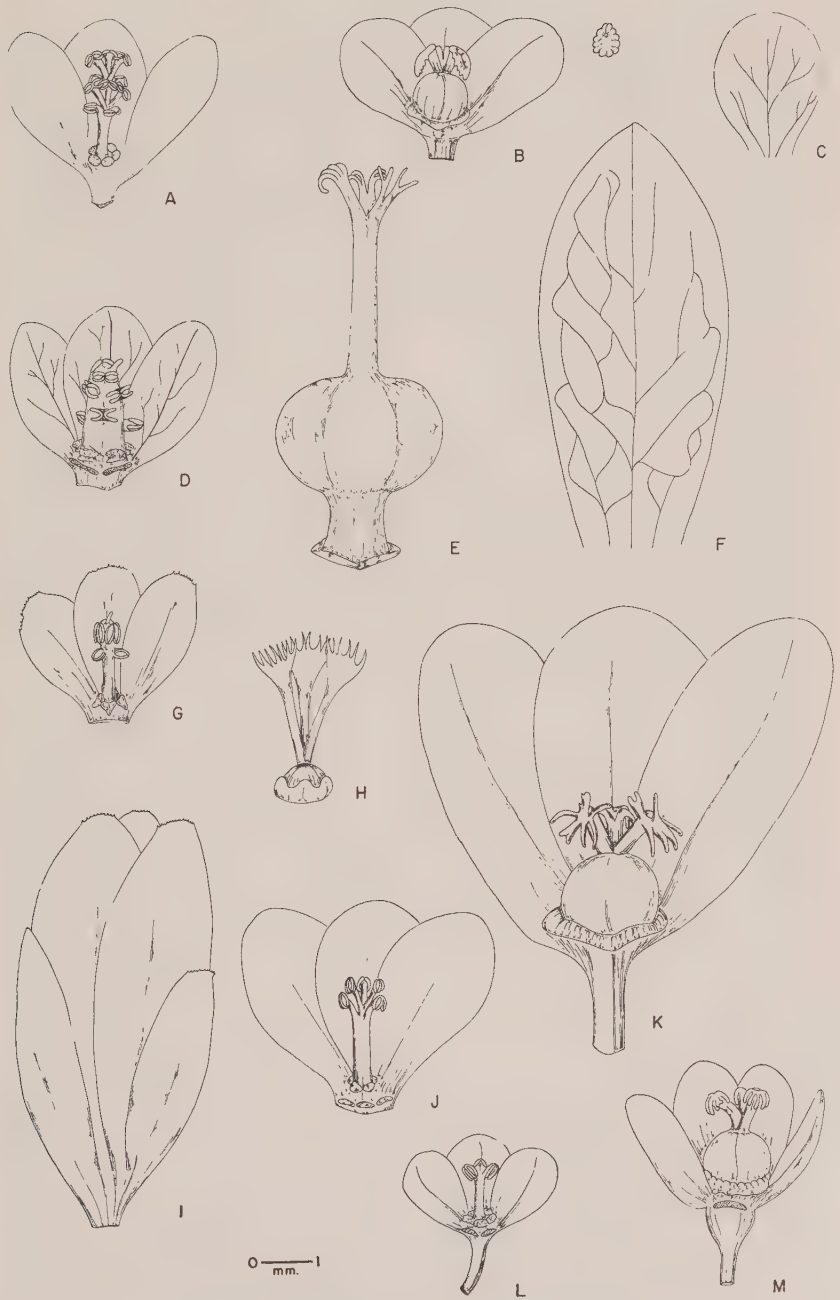
Stamen number	<i>P. discolor</i>	<i>P. pallidus</i>
18	0	1
17	0	2
16	0	2
15	0	6
14	1	4
13	12	6
12	17	7
11	6	9
10	8	5
9	4	1
8	1	4
7	1	1
6	0	1

* The figures in the two right-hand columns refer to the number of flowers having the specific stamen number. The mean number of flowers scored per collection was about 3, but there was some variation due to differences in the number of available male flowers on the specimens; this inequality in sampling may be partially counteracted by the considerable spread of variation on each plant (e.g., from 9–14 in one individual of *P. discolor*). It should be noted that the *P. pallidus* column includes collections of various transitional forms, or in other words all specimens from the Cajalbana area which are not obviously “good” *P. discolor*.

must be due to comparatively recent changes in the distribution of one or both species and, most probably, to a spread of *P. discolor* into the restricted range of *P. comptus*. It is interesting that there is no evidence of crossing between *P. discolor* and *P. orbicularis* of sect. *Orbicularia*, although the latter is also present near almost every station of *P. discolor* and shows an affinity (via *P. microdictyus*) evident enough so that crossing would *a priori* not appear impossible. Presumably there is a much stronger genetic barrier between *P. discolor* and *P. orbicularis* than between the former and *P. comptus*; this offers an interesting subject for further analysis on cytological lines.

PLATE XXV. FLOWERS OF SECT. *Williamia*, SUBSECTS. *Discolores* AND *Incrustati*.

FIGS. A–C. Male flower, female flower, and female calyx-lobe of *Phyllanthus discolor* Poepp. ex Spr. (Webster *et al.* 250 [GH]). FIGS. D–F. Male flower, gynoeceum, and female calyx-lobe of *Phyllanthus microdictyus* Urb. (Marie-Victorin & Clement 21525 [A]). FIGS. G–I. Male flower, gynoeceum, and female calyx of *Phyllanthus williamoides* Griseb. (Webster 4014 [GH]). FIGS. J–K. Male and female flowers of *Phyllanthus excisus* Urb. (Ekman 4055 [S]). FIGS. L–M. Male and female flowers of *Phyllanthus incrustatus* Urb. (Ekman 3848 [S]).



WEBSTER, WEST INDIAN PHYLLANTHUS

49. *Phyllanthus microdictyus* Urb. Symb. Ant. 9: 183. 1924.

(PLATE XXV, figs. D-F; PLATE XXVII, fig. A).

A shrub c. 1 m. high with the habit of a miniature tree, the stem simple or sparsely branching near the top; bark smooth, dark brownish, becoming finely fissured on old stems but not breaking up into plates. Cataphylls deciduous: stipules triangular-lanceolate, mostly 3-4 mm. long and (1.1-) 1.5-1.7 mm. broad (smaller on weak shoots), acute, truncate at the thickened base, lightly keeled, dark brown and scarious-indurate; blade narrowly lanceolate, acuminate, c. 2.5-3 mm. long. Branchlets (6-) 9-17 (-19) cm. long, 0.9-1.5 mm. thick, brownish, smooth and pruinose, usually flattened, with (6-) 8-12 (-14) leaves; first internode (15-) 20-40 (-45) mm. long, median internodes c. 10-20 mm. long. Leaves: stipules linear-lanceolate, acuminate, (1.5-) 2.5-3 mm. long, 0.4-1 mm. broad, scarious, deciduous. Petiole 2.5-4.5 mm. long, subterete, brownish. Leaf-blades flexibly chartaceous, ovate or elliptic, (1.5-) 2.5-5 (-6.5) cm. long, (1.3-) 2-3.5 (-4) cm. broad, emarginate (or less commonly obtuse or rounded) and minutely and inconspicuously apiculate at the tip, mostly rounded to cordate at the base; above dull green (bright red when first expanded), minutely foveolate, the midrib incised, the main laterals raised, repeatedly branching and anastomosing to form a fine raised reticulum with straight-sided meshes; beneath greyish-pruinose, the midrib raised, the laterals (c. 4 or 5 on a side) and ultimate veinlets very slightly raised, pale, forming a fine and inconspicuous reticulum; margins plane, not thickened.

Monoecious; usually the proximal 2 or 3 nodes of a branchlet with male cymules of 1-3 flowers, the succeeding nodes with bisexual cymules of 1 central female and 1 or 2 lateral male flowers.

Male flower: pedicel capillary, (5-) 7-15 mm. long. Calyx greenish white, sometimes pinkish tinged: calyx-lobes 6 (rarely 5), chartaceous, subequal, oblong to obovate, 2.5-3.5 mm. long, 1.3-2.3 mm. broad, entire and rounded at the tip, faintly triplinerved or the midrib pinnately branched. Disk-segments 6 (rarely 5), round or trigonous, smooth and entire, c. 0.25-0.45 mm. broad. Stamens 6-10 (-11), the filaments 1-1.7 mm. long, connate into a rather stout column; anthers subsessile (the free portion of the filament no longer than the anther) or the terminal ones short-stalked, inserted on the column spirally or in 2 or 3 whorls, ascending or spreading, c. 0.25-0.3 mm. long, 0.4-0.5 mm. broad; anther-sacs more or less divergent, globose before anthesis, dehiscing horizontally or obliquely, the slits apically contiguous but not confluent; pollen grains 20-24 μ in diameter, with c. 7 or 8 areoles per amb.

Female flower: pedicel capillary, (5-) 7-12 (-14) mm. long. Calyx colored as in the male; calyx-lobes 6 (rarely 7), strongly convex, subequal or unequal (the outer one or two lobes often manifestly shorter than the innermost), oblong to obovate, the larger lobes 7-8.5 mm. long, 3.5-5 mm. broad, entire and obtuse or rounded at the apex, 3-5-nerved from the base, the laterals ascending and anastomosing in a rather conspicuous net. Disk 5-angled, fairly massive in the bud but becoming fused with

and incorporated into the massive gynophore. Ovary oblate-spheroidal, about as high as (or somewhat higher than) the gynophore, pruinose; styles erect, (3.5–) 4–5 mm. high, connate $\frac{1}{2}$ to $\frac{3}{4}$ their length, gradually dilated at their ends into conspicuously lacerate 3- or 4-parted tips.

Capsule oblate, emarginate at the apex, c. 5 mm. in diameter, smooth, reddish brown, held within the erect appressed calyx-lobes. Columella conical, somewhat constricted at the tip, 2.2–2.4 mm. long. Seeds [those examined not quite mature] plano-convex, 2.5–2.7 mm. long, 1.5–1.6 mm. radially and tangentially, dark shiny reddish brown, nearly smooth (minutely colliculose); hilum submedian, triangular, light brown.

Flowering and fruiting April through July and possibly later, but apparently sterile during the winter.

TYPE: Cuba, *Ekman 3705*.

DISTRIBUTION: lowlands near the coast, northeastern Oriente Province, Cuba (MAP XXII).

CUBA. ORIENTE: Moa region, Cayoguan, *Acuña 12478* (SV [Herb. Roig n. 8593], US); Mina Cromita, Cayoguan, south of Punta Gorda, *Clemente & Alain 4074* (MICH); Rio Cayoguan, près du pont sur le chemin de la mine Delta, *Marie-Victorin & Clement 21525* (A, MT), *21749* (MT); same locality, cut-over forest of *Clusia*, *Bactris*, *Arthrostylidium*, et al., *Webster 3809* (GH, MICH); ad Taco Bay prope Baracoa in pinetis, 2 December 1914, *Ekman 3705* (S, HOLOTYPE; NY, ISOTYPE fragment and photograph; sterile).

A very distinctive and well-marked species, *P. microdictyus* appears to be quite restricted in range; the first four collections cited are all essentially from the same locality, so that there are, in effect, only two known stations. Although Ekman's type specimen is sterile, the characteristic venation of the leaves — identical with that of the fertile collections from Moa — leaves no doubt as to the identity or typification of the species. Ekman's designation of the Taco Bay collection as being from pinelands suggests a somewhat different habitat from the flood-plain woods along the Río Cayoguan, but the species would in any case appear to be a relatively mesophytic one.

Because of their evolutionary significance, the several affinities of *P. microdictyus* deserve special mention. Its large female flowers with long styles and stipitate ovary are so similar to those of the South American *P. salviaeifolius* that there can be little doubt of a fairly close relationship, although the latter species differs vegetatively by having hirsutulous axes and acuminate, more coarsely veined leaves. However, *P. microdictyus* is also an obviously near relation of *P. discolor*, which it greatly resembles vegetatively. Furthermore, the incipient production of mesophyllar sclereids in *P. microdictyus* presages their full development in *P. cristalensis*; and since it would appear that it is through the latter (or a similar species) that the highly specialized representatives of subsect. *Incrustati* and sect. *Orbicularia* have originated, it would not be incorrect to regard *P. microdictyus* as the progenitor of this entire phylogenetic line.

50. *Phyllanthus cristalensis* Urb. Repert. Sp. Nov. 28: 212–213. 1930.

Glabrous shrub up to 1.5 m. high; branches shiny reddish brown, becoming grey with age, c. 1.5–3 mm. thick. Cataphylls black, indurate, soon deciduous: stipules lanceolate, c. 1.5–2 mm. long, acuminate, entire; blade narrower. Branchlets mostly 4–11 cm. long, 0.5–0.8 mm. thick, smooth, reddish brown, subterete (slightly compressed proximally), with 8–15 leaves; first internode c. 5–15 mm. long, median internodes 4–7 mm. long. Leaves: stipules reflexed, subpersistent, triangular-lanceolate, 1.7–2 mm. long, 0.7–1.1 mm. broad, rather blunt at the tip, entire, dark brown, somewhat indurate. Petiole 1.5–2.5 mm. long, slightly flattened, dark brown, nearly smooth. Leaf-blades coriaceous, broadly elliptic to sub-orbicular, c. 1–2.2 cm. long, 0.8–1.9 cm. broad, emarginate and with a deciduous apiculum at the tip, rounded to emarginate at the base; above dull brownish olivaceous, mottled (the cell outlines of the irregularly anastomosing veins visible under a lens), the subprominent midrib plane or sunken, the laterals rather obscure; beneath greyish or brownish, the midrib and laterals (c. 4 or 5 on a side) plane, not very prominent, the reticulum obscure; margins plane, scarcely thickened.

Monoecious (presumably); flowers [and fruit not seen, description ex Urban] few, solitary or paired, pedicels 3–5 mm. long.

Male flower: calyx-lobes 5, narrowly ovate, 2 mm. long, barely 1 mm. broad; stamen number not determined; filaments connate, anthers discrete. Female flower: pedicel narrowly obconic-thickened above; calyx-lobes 5, narrowly ovate, 2 mm. long; styles not seen.

Capsule oblate, rounded-trigonus, c. 4 mm. in diameter; seeds brownish, minutely punctulate, c. 2 mm. long, 1.7 mm. broad.

TYPE: Cuba, *Ekman 15993*.

DISTRIBUTION: endemic to the Sierra Cristal, eastern Cuba (MAP XXII).

CUBA. ORIENTE, Sierra Cristal: at the tributary of the Río Lebisa in charascales, alt. 600–1100 m., 15 Dec. 1922, *Ekman 15967* (S); in low *Arthrostyidium* thickets which cover the top, alt. 1100–1325 m., 15 Dec. 1928, *Ekman 15993* (NY, ISOTYPE); ridge west of Pico Cristal, mossy elfin forest, 4 Mar. 1954, *Jervis 3206* (GH).

Although still poorly known, *P. cristalensis* is evidently a very distinct species on the basis of its vegetative characters. Vegetatively it is intermediate between subsects. *Discolores* and *Incrustati*, having the smooth axes of the former combined with the highly sclerified leaves of the latter. However, until adequate flowering material can be collected its relationships cannot be satisfactorily determined.

Subsect. 16b. *Incrustati*, subsect. nov.

Phyllanthus sect. *Williamiandra* Griseb. Goett. Nachr. 1865: 171. 1865.

Ramsdenia Britton, Mem. Torr. Bot. Club 16(2): 72. 1920.

Stems and branchlets incrustate with dark bran-like flakes of bark:

leaves of branchlets alternate, coriaceous (heavily sclerified within); stamens (2-) 3-6; styles erect, conspicuously lacerate.

TYPE SPECIES: *Phyllanthus williamioides* Griseb.

Grisebach proposed to distinguish sect. *Williamiandra* on the basis of its androecium and styles, but his description of the androecium is erroneous and his discussion misleading. The type species, *P. williamioides*, has only 5 or 6 stamens (not 10 as reported by Grisebach), and the conical apex of the staminal column cannot serve as a sectional character since it does not occur in the two related species. Grisebach's stated distinction between the styles of *Williamiandra* (correctly likened to those of sect. *Oxalystylis*) and those of sect. *Williamia* is wholly incorrect, for he erroneously describes the styles of the latter as bifid. Except for the difference in stamen number, there are no floral characters available for separating *Williamia* from *Williamiandra*; but since the species of the two groups can be distinguished vegetatively, it seems appropriate to place them into two subsections of the inclusive sect. *Williamia*.

Britton's proposed genus *Ramsdenia*, which included *P. excisus* and *P. incrustatus*, corresponds almost exactly to the present subsection; he did not discuss its relationships or clearly define its characters, and he was apparently unaware of the existence of *P. williamioides*.

51. *Phyllanthus williamioides* Griseb. Goett. Nachr. 1865: 169-170. 1865; Muell. Arg. in DC. Prodr. 15(2): 328-329. 1866.

(PLATE XXV, figs. G-I).

Diasperus williamioides (Griseb.) O. Ktze. Rev. Gen. 2: 601. 1891.

A small shrub 0.5-1.5 (-2) m. high, with two or more stems clustered on a gnarled caudex (stem unbranched in young plants); bark of stem-base and root broken up into conspicuous patterns of squares. Stems and branchlets incrustate but the bark-platelets smooth and glabrous, dark brown, the exposed spongy tissue reddish brown. Cataphylls blackish, indurate but mostly soon deciduous: stipules lanceolate, (1.5-) 1.8-2.7 mm. long, 0.7-1.2 mm. broad; blade c. 1.8-2.5 mm. long, 0.5 mm. broad. Branchlets erect or spreading, (5-) 8-15 (-19) cm. long, 1-1.2 mm. thick, reddish-brown- or blackish-incrustate, terete or angled, with mostly 10-25 (-35) leaves; first internode (5-) 7-12 (-16) mm. long, median internodes 2-6 (-10) mm. long. Leaves: stipules acicular-lanceolate (convexly conduplicate), soon deciduous, 2.5-3.5 (-5) mm. long and 0.5-1 mm. broad, rather blunt at the tip, chartaceous, dark brown. Petiole 1.5-2.5 mm. long, brownish, smooth, flattened. Leaf-blades coriaceous, mostly orbicular or nearly so (sometimes slightly obovate or broader than long), (1-) 1.5-2.5 cm. long, (1-) 1.3-2.2 cm. broad, retuse or emarginate at the tip, cordate at the base; above olivaceous and subglucid or dully plumbeous, minutely foveolate-reticulate, the midrib slightly incised, the lateral veins and veinlets forming a fine slightly raised reticulum; beneath brownish- or olivaceous-plumbeous (minutely white-dotted with wax-covered stomata), the midrib plane, the slightly raised laterals (c. 5 or 6 on a side) anas-

tomosing with the conspicuous tertiary veinlets to form a close reticulum; margins plane, not thickened.

Monoecious, flowers in axillary bisexual cymes; central flower female, lateral ones male (the male mostly developing after fruiting calyx has fallen, so that the arrangement on the branchlet appears to be of proximal racemes of male flowers and distal solitary female flowers); bracteoles blackish and indurate.

Male flower: pedicel c. 1.8–2 mm. long. Calyx greenish white, whitish, or reddish tinged; calyx-lobes 5, thin but coriaceous, subequal, oblong to spatulate, (1.3–) 1.5–2.3 mm. long, 0.7–1.5 mm. broad, denticulate near the apex, more or less triplinerved but nerves rather obscure. Disk-segments 5, flattened or concave, roundish or triangular, smooth and entire, 0.25–0.35 mm. broad. Stamens 5 or 6, the filaments connate into a relatively slender column 1–1.1 mm. high and 0.25–0.4 mm. thick; anthers in two series, the upper of 3, the lower of 2 or 3, the apex of the column terminated by an apiculum; anthers slightly apiculate, sessile on the column or very nearly so, the upper erect, the lower ascending or spreading, c. 0.3–0.4 mm. long and broad; anther-sacs sub-parallel, dehiscing longitudinally, the slits not confluent; pollen grains 24–27 μ in diameter, the areoles polybrochate, c. 5–6 μ across, c. 10 per amb.

Female flower: pedicel short and stout, only (0.7–) 1.2–1.8 (–2.4) mm. long. Calyx colored as in the male; calyx-lobes 5–7, quite unequal, denticulate at the apex, incrassate at the base, nerves several but obscure; outer lobes oblong, obtuse, 2.5–3.5 mm. long, 1.5–2 mm. broad; inner lobes obovate, rounded at the tip, 5–5.5 mm. long, 2.2–2.8 mm. broad. Disk a thick brownish crenate-rimmed cup, enclosing the base of the ovary. Ovary sessile, smooth, carinate between the septae; styles erect, free, 1.8–2.7 mm. high, the dilated tips more or less 3-fid, the three branches with a total of c. 8–10 slender lacerae.

Capsule subglobose, c. 4 mm. in diameter, the valves olivaceous, smooth, not veiny, 3.5 mm. long, often retained within the appressed calyx-lobes. Columella 2.2 mm. long. Seeds trigonous, somewhat asymmetric (excentrically carinate on the back), 2.2–2.3 mm. long, 1.2–1.5 mm., radially and tangentially, blackish brown, colliculose on back and sides; hilum subterminal, elliptic or ovate, c. 0.5 mm. long.

TYPE: Cuba, *Wright 1944*.

DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

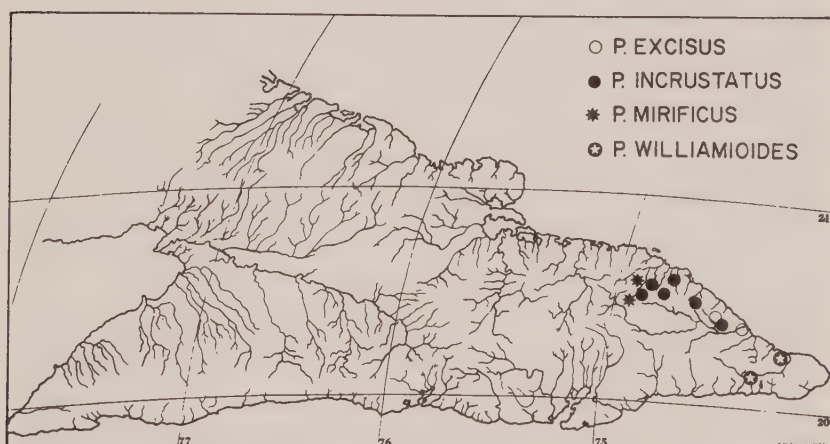
CUBA. ORIENTE: Cuchillas de Baracoa, *Wright 1944* (GOET, HOLOTYPE; GH, ISOTYPE; locality ex isotype); Altos de Farola, c. 20 miles south of Baracoa, pineland at 1750 ft., 3 Aug. 1951, *Webster 4014* (GH, MICH, NY); among pines and tree ferns, moist arroyo c. 12 miles east of Baracoa, 18 Mar. 1954, *Jervis 3332* (GH).

Wright's type collection differs from the other specimens in its distinctly obovate leaves. However, in the field, leaves of this shape were found on shoots from the base of plants which higher up bore orbicular leaves; it

thus appears that Wright made his collection from a stump sprout or very depauperate plant.

The present species is very closely related to *P. incrustatus*, but is usually distinguishable at first sight by virtue of its smooth bark platelets (these usually scabridulous in *P. incrustatus*) and larger more elongated leaves. Actually, the concave deciduous stipules and androecium of 5–6 stamens are the best diagnostic features of *P. williamioides*, and will always permit its ready separation from *P. incrustatus*.

As in many species of subg. *Xylophylla*, the leaves of *P. williamioides* are distinctly reddish-tinged when young, though less strikingly so than in *P. pachystylus*. The undersurface is pale yellow at first and only later becomes green; this behavior, again, is characteristic of many other species.



MAP XXIII. Distribution of sect. *Willamia* subjects. *Incrustati* and *Mirifici* in eastern Cuba.

52. *Phyllanthus excisus* Urb. Repert. Sp. Nov. 13: 449–450. 1914.
(PLATE XXV, figs. J–K).

Ramsdenia excisa (Urb.) Britton, Mem. Torr. Bot. Club 16(2): 72. 1920.

Shrub c. 2–3 m. high; pith brownish; stems and branchlets incrustate with smooth dark reddish brown platelets, the interspaces of spongy tissue light reddish brown. Cataphylls blackened, indurate, more or less persistent: stipules triangular-lanceolate, 2–2.5 mm. long, 1.5–1.6 mm. broad, acuminate; blade narrower. Branchlets stout, 9–27 cm. long, 1.7–3 mm. thick, reddish brown and incrustate, subterete (more or less angled distally), with (10–) 15–35 nodes; first internode (5–) 10–15 (–20) mm. long, median internodes 5–18 mm. long. Leaves: stipules lanceolate, 2.5–3 mm. long, 1.1–1.5 mm. broad, acuminate, quite oblique at the base, blackish, indurate, appressed or spreading, persistent. Petioles 1.5–3 mm. long, brownish, transversely furrowed, with a deep median adaxial groove.

Leaf blades coriaceous, mostly ovate or elliptic, (2.5-) 3-4.5 cm. long, 2.5-3.5 cm. broad, emarginate at the tip, obtuse to subcordate at the base; above olivaceous-plumbeous, minutely foveolate-reticulate, the midrib plane or slightly impressed, the lateral veins obscure; beneath brownish grey when dried (not white-dotted), the midrib saliently raised, the laterals (c. 6-8 on a side) and tertiary veinlets slightly raised, anastomosing to form a rather prominent reticulum; margins unthickened, plane.

Monoecious; flowers in axillary bisexual cymules, each of a solitary central female flower and a few (c. 3 or 4) male flowers on bracteolate lateral axes; bracteoles indurate, persistent in old axils.

Male flower: pedicel capillary, c. 4-5.5 mm. long. Calyx whitish (ex Shafer); calyx-lobes 5, subequal, oblong to obovate, (3-) 3.3-4 mm. long, 1.5-2 mm. broad, entire, the venation obscure. Disk-segments 5, roundish, entire, c. 0.4-0.5 mm. across. Stamens 5-6, filaments united into a rather stout non-apiculate column 1.5-1.8 mm. high and 0.5-0.6 mm. broad; anthers biseriate (upper series of 3, lower of 2 or 3) but both whorls crowded at the top, not evidently apiculate; anther-sacs subparallel, dehiscing longitudinally, the slits not confluent; pollen grains 19-22 μ in diameter, the areoles polybrochate, c. 7-11 μ long, 4-5 per amb.

Female flower: pedicel nearly straight, slender, (10-) 12-15 mm. long. Calyx greenish-white (ex Shafer); calyx-lobes 5, coriaceous, thickened at the base, subequal (the outer slightly narrower), oblong to obovate, the larger lobes 5-7 mm. long [up to 8 mm., ex Urb.], 2.5-4.5 mm. broad, entire and rounded at the tip, the venation obscure. Disk massive, obtusely 5-angled, entire (or minutely crenulate), obscurely foveolate, the margin plane, somewhat thinner. Ovary sessile, carinate dorsally; styles erect, free or shortly connate at the base, 1.8-2 mm. high, the dilated ends deeply parted into 6-7 (-10) narrow divaricate lacerae; outline of stylar apex roughly triangular, two arms extending adaxially, the third abaxial and with more lobes.

Capsule subglobose, emarginate, c. 5 mm. in diameter, smooth or slightly rugulose, brownish, not veiny. Columella c. 3 mm. long. Seeds [seen only in immature condition] c. 3 mm. long, brownish, probably with the ornamentation of *P. williamioides* when mature.

TYPE: Cuba, *Shafer 4447*.

DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Navas to Camp Buena Vista, alt. 650 m., 23 March 1910, *Shafer 4447* (NY, LECTOTYPE; F, MO, US, ISOTYPES); prope Baracoa, ad Maraví in pinetis, 26 Dec. 1914, *Ekman 4055* (S).

Apparently a rare species of restricted range, *P. excisus* is well distinguished from the two related species of subsect. *Incrustati* by its larger ovate leaves, larger flowers on longer pedicels, and different styles. Its

strong resemblance to *P. microdictyus* of subsect. *Discolores* can hardly be mere coincidence, and it can be rather confidently regarded as a xerophytic derivative of that plant. The flowers of both species are similar, but *P. excisus* has fewer stamens and, of course, its incrustate stems and coriaceous leaves easily separate it from *P. microdictyus*.

The apparent rarity of *P. excisus*, as compared with the other Oriente species of sect. *Williamia*, may prove to be illusory, for the region between Navas and Baracoa has been much less visited by collectors than the Moa district, which up until recently was much more accessible.

53. *Phyllanthus incrustatus* Urb. Repert. Sp. Nov. 13: 449. 1914.
(PLATE XXV, figs. L-M).

Ramsdenia incrustata (Urb.) Britton, Mem. Torr. Bot. Club 16(2): 73. 1920.

Shrub 0.5–2 m. high; stems and branchlets usually scabridulous-hirtellous at the tips, below incrustate with scabridulous platelets of bark (rarely the platelets smooth). Cataphylls blackish, indurate, subpersistent: stipules triangular to narrowly lanceolate, (1–) 1.5–3.7 mm. long, 0.5–1 mm. broad, acute to acuminate (sometimes with very attenuate tips), sometimes excentrically keeled, becoming reflexed or spreading; blade narrowly lanceolate, (0.7–) 1.5–3.5 (–5) mm. long, also more or less reflexed. Branchlets (5–) 7–17 (–26) cm. long, 1–1.7 mm. thick, incrustate with dark brown usually scabridulous platelets separated by lighter reddish brown furrows, with (10–) 15–40 (–60) leaves; first internode 3–10 mm. long, median internodes 2–6 mm. long. Leaves: stipules persistent, appressed or reflexed, triangular to linear-lanceolate, (0.8–) 1.2–2.5 (–3.2) mm. long, 0.3–0.9 mm. broad, acute or acuminate, dark brown, more or less indurate. Petiole 1–1.8 mm. long. Leaf blades coriaceous, mostly orbicular or suborbicular (sometimes broader than long), c. 7–12 (–15) mm. long, 6–12 (–14) mm. broad, usually retuse or emarginate and inconspicuously apiculate, truncate or more commonly cordate at the base; above dull olivaceous or plumbeous, minutely foveolate-reticulate, the midrib impressed, the laterals usually rather obscure; beneath greyish brown or purplish brown (minutely white-dotted with wax-covered stomata), the slightly raised laterals (c. 5 or 6 on a side) anastomosing with the veinlets to form an inconspicuous reticulum; margins plane, not thickened.

Monoecious; flowers in axillary bisexual cymules; first (central) flower of cymule female, rapidly maturing and deciduous, succeeded by several male flowers on one or both lateral abbreviated axes; branchlets thus appearing (as in *P. williamoides*) to have short racemes of male flowers at proximal nodes and solitary female flowers at distal nodes.

Male flower: pedicel (0.5–) 1–1.5 mm. long. Calyx whitish (in living condition [ex Shafer], reddish when dried); calyx-lobes 5, subcoriaceous but thin, subequal, oblong to obovate or spatulate, (1.3–) 1.5–2.4 mm. long, (0.7) 1–1.5 mm. broad, rounded at the tip, entire or occasionally denticulate, nervation obscure, only the midrib at all prominent. Disk-

segments 5, flattened or concave, roundish or trigonous, c. 0.25–0.35 mm. across. Stamens 3 or 4 (rarely 2), filaments connate into a slender non-apiculate column 0.6–1.2 mm. high and 0.15–0.25 mm. thick; anthers sessile, aggregated into a mass at the top of the column, 0.25–0.35 mm. long; anthers-sacs parallel, dehiscing longitudinally and vertically, the slits not confluent; pollen grains 12–19 μ in diameter, the areoles polybrochate, c. 6–7.5 μ long, c. 3–5 per amb.

Female flower: pedicel slender or incrassate above the middle, 1–3 mm. long. Calyx colored more or less as in the male; calyx-lobes 5, rather unequal, rounded at the tip, entire, the outer oblong, 1.6–2.7 mm. long and 0.8–2.3 mm. broad, the inner mostly spatulate or obovate, 1.8–3.3 mm. long and 1.2–3.3 mm. broad; nervation obscure. Disk massive, 5-angled, entire, plane, foveolate. Ovary sessile; styles free or shortly connate below, spreading or ascending, flattened, 0.5–0.6 mm. long, the dilated apices 5–6-lacerate.

Capsule subglobose, emarginate, c. 3–4.5 mm. in diameter, the valves smooth, dark brown, not veiny. Columella 1.5–2 (–2.5) mm. long. Seeds trigonous, asymmetrically carinate on the back, 1.8–2.7 mm. long, 1.1–1.8 mm. radially, 1.35–1.45 mm. tangentially, reddish brown, nearly smooth.

TYPE: Cuba, *Shafer 4020* (NY, LECTOTYPE; the original specimen of this collection in Herb. Krug & Urban destroyed during World War II).

DISTRIBUTION: wooded areas, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Cumbre Cayo [Cayoguan], *Acuña 12477* (US); Mina Delta, c. 500 m. alt., échine de serpentine sur le chemin de la mine Delta, *Marie-Victorin & Clément 21754* (A, MT); Camp La Gloria, south of Sierra Moa, *Shafer 8113* (F, MO, NY, US); damp thickets between Río Yamanigüey and Camp Toa, alt. 400 m., 22–26 Feb. 1910, *Shafer 4020* (NY, LECTOTYPE); moist woods, Navas to Camp Buena Vista, alt. 650 m., *Shafer 4453* (NY, US); Minas de Iberia ad Taco Bay, alt. c. 800 m., *Ekman 3833, 3848* (S).

Evidently the commonest and most widespread of the three species of the subsection, *P. incrustatus* is morphologically the most specialized, at least with respect to its smaller leaves and androecium of fewer stamens. Although occasional large-leaved forms, such as *Ekman 3848*, simulate *P. williamioides*, the ensemble of characters of *P. incrustatus* is distinctive. In addition to its smaller leaves and fewer stamens, it also differs from *P. williamioides* in its persistent stipules and somewhat larger number of leaves per branchlet.

Although its small, roundish, coriaceous leaves suggest an affinity of *P. incrustatus* with the species of sect. *Orbicularia*, it does not appear likely that *P. incrustatus* is the progenitor of that group. Rather, it seems that the species of subsect. *Incrustati* represent a more or less parallel line of development with the representatives of *Orbicularia*.

Subsect. 16c. *Mirifici*, subsect. nov.²¹

Stems and branchlets smooth but with conspicuous lenticels; leaves of branchlets opposite, coriaceous (heavily sclerified within); stamens 5; styles obsolete, the greatly dilated stigmas (style-tips) forming a cap which covers most of the ovary.

TYPE SPECIES: *Phyllanthus mirificus* Webster.

The single very distinctive species of this monotypic taxon, only recently discovered in eastern Cuba, is unique among the New World species of *Phyllanthus* in its opposite leaves (on the branchlets) and hypertrophied stigmas. Although its leaf arrangement and androecium suggest certain Old World taxa, its areolate pollen grains, leaf structure, and aspect provide an incontestable basis for placing it in sect. *Williamia*. Its affinity with sect. *Incrustati* is evident from even superficial comparison, but its many distinctive characters amply justify the erection of a special subsect. *Mirifici*.

54. *Phyllanthus mirificus* Webster, Contr. Gray Herb. 176: 58. 1955.
(PLATE XXVI, figs. A-C).

Definitely woody, presumably a shrub; branches slender, terete, not over 3 or 4 mm. thick (toward the ends), smooth, greyish- or reddish-brown, with conspicuous elliptic to linear lenticels. Cataphylls blackish and indurate but soon deciduous: stipules triangular-lanceolate, 2.3-3 mm. long, 1-1.5 mm. broad, acuminate, entire, carinate on the back; blade linear-lanceolate, c. 2 mm. long. Deciduous branchlets 8-13.5 cm. long, 1.5-2 mm. thick (those on lateral axes only 1 mm. thick), terete, smooth, brownish, becoming lenticellate proximally or throughout, with c. 6-8 (-11) pairs of leaves; first internode 6-20 mm. long, median internodes 3-20 mm. long. Leaves of branchlets all opposite (one node very slightly higher than its neighbor): stipules blackish and indurate but mostly soon deciduous, triangular-lanceolate, 2.2-3 mm. long, 0.6-0.9 mm. broad, acuminate, entire. Petioles 1.8-3 mm. long, brownish, plane and grooved down the middle adaxially, convex and corrugate-rugulose abaxially. Leaf-blades rigidly coriaceous, elliptic or ovate to suborbicular, 1.5-2.8 cm. long, 1.3-2.1 cm. broad, emarginate at the apex (the small short-conical dark brown apiculum of the juvenile leaf represented by a scar, or apparently absent), obtuse or rounded to subcordate at the base; above olivaceous or brownish, the midrib conspicuous, pale, plane or slightly sunken, the laterals obscured by the close-meshed slightly raised reticulum of tertiary veinlets; beneath more or less greyish-pruinose, the midrib nearly plane, the laterals (c. 5 or 6 on a side) and veinlets anastomosing in a sub-prominent reticulum; margins sharply differentiated, thin and acute, plane or reflexed (but not revolute).

²¹ Subsect. *Mirifici*, subsect. nov. Ramis ramulisve lenticellatis; foliis ramulorum oppositis, coriaceis; staminibus 5; stigmatibus dilatatis, calyptratis.—Species typica *Phyllanthus mirificus* Webster.

Monoecious; flowers in axillary bisexual cymules, each with a solitary female and mostly 2 or 3 male flowers; bracteoles ovate, blackish and indurate, persistent.

Male flower: pedicel slender, c. 1–1.2 mm. long. Calyx reddish when dried; calyx-lobes 5, chartaceous, obovate, c. 1.5 mm. long, 0.9–1.3 mm. broad, rounded at the tip, entire, the midrib apparently unbranched. Disk-segments 5, ellipsoid, somewhat thickened, entire, c. 0.25–0.3 mm. across. Stamens 5; filaments connate into a column c. 0.5–0.8 mm. high, unequal in length (two anthers inserted lower than the other three); anthers subsessile, ascending or vertical, blunt, 0.3–0.4 mm. long, 0.4–0.45 mm. broad; anther-sacs divergent, dehiscing vertically, the slits not confluent; pollen grains 16–18 μ in diameter, areoles polybrochate, c. 6 μ across, c. 5–7 per amb.

Female flower: pedicel (at anthesis) 1.5–2.5 mm. long, subterete, enlarged and massive above. Calyx reddish when dried; calyx-lobes 6, subequal, biseriate, the outer broadly ovate, the inner broadly obovate, c. 1.5–1.8 mm. long, 1.1–1.4 mm. broad, entire, the veins obscure. Disk rather massive, bluntly angled, plane, the margins entire. Ovary subglobose, sessile, almost completely covered by the lower margins of the three dilated stigmas (style-ends) which are reflexed and appressed to form a close-fitting calyptra; stigmas with auricles connivent into a blunt beak at the top, the lateral margins entire, the distal margins crenulate-notched, 0.9–1.1 mm. long, 0.9–1 mm. broad across the distal edge.

Fruit and seeds unknown.

TYPE: Cuba, *León et al.* 22613.

DISTRIBUTION: scrublands and pinelands, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Charrascal del Coco, south of Moa, July 1945, *León, Clemente, & Alain* 22613 (MICH, HOLOTYPE; LS, ISOTYPE); charrascos y pinares, Sierra de Moa, alt. c. 750 m., 25 July 1953, *Alain* 3380 (GH); pineland barrens, Charrascos de Peña Prieta, Toa, alt. 600 m., 30 Dec. 1953, *Alain* 3616 (GH; sterile).

This extraordinary species, which remained undetected up until recent times, now appears to be as widely distributed in the Sagua-Baracoa range as some of the other specialized members of sect. *Williamia*. Its opposite branchlet-leaves and calyptriform stigmas at once set it apart from all of its West Indian congeners, and its androecium of 5 stamens in two unequal sets appears very similar to that in certain Old World species of subg. *Kirganelia*. Nevertheless, its phyllanthoid branching and areolate pollen grains show that it belongs in subg. *Xylophylla*, and both foliar and floral characters attest its affinity with the species of sect. *Williamia*. However, no one species of the section appears particularly close to *P. mirificus*, although *P. excisus* has a similar aspect (the type collection was, in fact, determined as that species), while *P. williamiioides* has similar androecia and short-pedicellate flowers. In some ways, *P. mirificus* is

intermediate between subsects. *Discolores* and *Incrustati*; this is especially true of its development of copious lenticels, which presents a condition transitional between the smooth stems of subsect. *Discolores* and the scurfy axes of subsect. *Incrustati*. Because of this intermediary position and of its very divergent features, *P. mirificus* seems best assigned to a special subsection of its own.

Sect. 17. *Thamnocharis* Webster, Contr. Gray Herb. 176: 59. 1955.

Shrubs with phyllanthoid branching; cataphylls large, indurate; leaves coriaceous, stipules caducous. Monoecious; cymules bisexual, the flowers appearing with the expanding leaves. Male flower: calyx-lobes 4-6; disk-segments 4-6; stamens 2-6 (-8), filaments united (apparently free in *P. comptus*), anthers dehiscing vertically; pollen grains areolate. Female flower: calyx-lobes 4-6, coriaceous; disk entire, angled; styles free or connate, bifid, the style-branches narrowed to acute tips. Capsule subglobose, dry, not veiny; seeds smooth or rugulose.

TYPE SPECIES: *Phyllanthus cinctus* Urb.

The relationships and nomenclature of this Cuban section and its three constituent species were discussed at some length in the original place of publication (op. cit. pp. 59-62). However, subsequent investigation has shown (on the basis of the presumed hybridization between *P. discolor* and *P. comptus*) that there must be a fairly close affinity between sects. *Williamia* and *Thamnocharis*; consequently, the position of the latter in the linear arrangement of sections has been altered. Furthermore, it is now clear that sect. *Thamnocharis* need not be compared with the Asiatic sect. *Eriococcodes*, for the latter definitely belongs in subg. *Eriococcus*, and its floral similarities are simply due to parallel evolution. Despite the dissimilarity (in gross appearance and in floral details) between *P. cinctus* and *P. discolor*, a significant affinity between subsect. *Discolores* (of sect. *Williamia*) and sect. *Thamnocharis* appears highly probable.

Before male flowers of *P. comptus* and before its hybridization with *P. discolor* were known, sect. *Thamnocharis* was thought to be related to sect. *Epistylum*. The Jamaican species of that section resemble the Cuban species of sect. *Thamnocharis* in their palm-like habit, reduced androecium, and similarly veined leaves. It may yet be possible to show that sect. *Epistylum* is closely related to the Cuban plants, but since its representatives (*P. cauliflorus* and *P. cladanthus*) differ in having persistent stipules, horizontally dehiscing anthers, and dilated lacerate styles, they are placed at some distance in the present linear arrangement. Even more similar to sect. *Thamnocharis*, at least superficially, is the monotypic sect. *Glyptothamnus* which closely mimics *P. cinctus*; but that group appears to be much more closely allied to sect. *Epistylum* in its technical characters. These rather puzzling suggestions of reticulate relationships indicate that the phylogeny of the groups in question can by no means be considered finally settled.



WEBSTER, WEST INDIAN PHYLLANTHUS

KEY TO THE SPECIES

1. Calyx-lobes and stamens 5 or 6; styles free; pedicel of female flower 10–14 mm. long; seeds vermiculately marked, 4.5 mm. long or more; cataphyllary stipules ribless, less than 1 cm. long. 55. *P. comptus*
1. Calyx-lobes 4; stamens 2; styles united into a column; pedicel of female flower not over 6 mm. long; seeds smooth, not over 4 mm. long; cataphyllary stipules longitudinally ribbed, 1 cm. long or more.
 2. Male calyx-lobes c. 2 mm. long, with mostly 1–3 nerves from the base; anthers triangular, 0.5–0.8 mm. long; female calyx-lobes reflexed at the tips, the inner (longer) c. 3–5 (–6) mm. long; female disk tenuous, rim-like, c. 2 mm. across. 56. *P. cinctus*
 2. Male calyx-lobes c. 3–3.5 mm. long, with mostly 5–7 nerves from the base; anthers lanceolate, 0.9–1.2 mm. long; female calyx-lobes not reflexed at the tips, the inner (longer) becoming 6–8 mm. long; female disk very massive, forming a mound 3–4 mm. broad and 0.5–1 mm. high, its foveolate rim depressed. 57. *P. ekmanii*

55. *Phyllanthus comptus* Webster, Contr. Gray Herb. 176: 61. 1955.

Glabrous shrub; branches terete, smooth, pale brown becoming greyish, c. 3–4 mm. thick. Cataphylls massive and coriaceous but deciduous: stipules triangular-lanceolate, acuminate, c. 6–7.5 mm. long, 2–3 mm. broad, obliquely truncate at the base, brownish with blackened indurate tips; blade narrower. Deciduous branchlets (5.5–) 7–14 cm. long, 1–1.5 mm. thick, stramineous or pale reddish brown, smooth, subterete (somewhat flattened proximally), with only 5–7 nodes; first internode (15–) 20–30 mm. long, median internodes c. 15–30 mm. long. Leaves: stipules caducous, ovate-lanceolate, 5–6 mm. long, 2.7–3 mm. broad, acuminate, more or less denticulate along the margin, brownish, scarious-chartaceous with more or less indurate darkish tips. Petioles plane adaxially, convex abaxially, smooth, stramineous or reddish brown, 2.5–4 mm. long. Leaf-blade coriaceous, ovate or elliptic, c. (2.5–) 3–5.5 cm. long, (1.2–) 1.5–3 cm. broad, obtuse and minutely apiculate at the tip, obtuse or rounded at the base; above sublucid, olivaceous, the midrib and chief laterals slightly raised; beneath paler, the midrib and main laterals (4 or 5 on a side) slightly raised, forming a subprominent reticulum, veinlets obscure; margins cartilaginous-thickened, light brownish, more or less reflexed.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules usually bisexual, of 1 female and several (c. 5–8) male flowers.

 PLATE XXVI. FLOWERS OF SECT. *Williamia*, SUBSECT. *Mirifici*, AND OF SECT. *Thamnocharis*.

FIGS. A–C. Male flower, female calyx, and gynoecium of *Phyllanthus mirificus* Webster (*Alain* 3380 [GH]). FIGS. D–F. Male flower, female flower, and gynoecium of *Phyllanthus cinctus* Urb. (*Jervis* 3355 [GH]). FIGS. G–J. Male flower, androecium, female calyx-lobe, and gynoecium of *Phyllanthus ekmanii* Webster (*Jervis* 3037 [GH]).

Male flower (described from immature buds): pedicel up to c. 2.5 or 3 mm. long. Calyx-lobes 6 (rarely 5), greenish, nervation obscure; disk-segments 6 (rarely 5), flattened, foveolate; stamens (4-) 5 or 6 (-8), filaments shorter than anthers and apparently not united (but staminal column perhaps not yet developed); anthers reniform, c. 0.4-0.5 mm. broad; anther-sacs divergent, dehiscing more or less vertically, the slits apically confluent.

Female flower: pedicel slender, subterete below, gradually dilated and obtusely angled above the middle, 10-14 mm. long. Calyx-lobes 6 (rarely 5), unequal, spatulate, rounded and entire at the tip, in flower 2.5-4 mm. long and 1.2-1.7 mm. broad, in fruit 3.3-4.2 mm. long, c. 1.7 mm. broad, the nerves obscure. Disk flat, 6-angled, becoming dark brown, not conspicuous. Ovary reddish brown, sulcate, emarginate at the top; styles free except at the very base, ascending, c. 1.5 mm. high, bifid; style-branches divergent, recurving, terete, narrowed to the tips.

Capsule-valves c. 7-7.5 mm. long, reddish brown, the veins obscure. Columella 3.8-4 mm. long. Seeds trigonous, asymmetric, carinate or somewhat irregular on the back, (4.5-) 4.8-5.1 mm. long, (2.5-) 3 mm. tangentially (across the back), dark brown (to the naked eye), with a vermiculate pattern of brownish-black raised lines on a light brown background; hilum submedian, c. 0.4-0.5 mm. across, the raphe conspicuous.

TYPE: Cuba, *Acuña* 18222.

DISTRIBUTION: endemic to the Cajalbana region, Pinar del Río province, Cuba (MAP XXIV).



MAP XXIV. Distribution of sect. *Thamnocharis* in Cuba.

CUBA. PINAR DEL RÍO: en arroyos, La Cajalbana, La Mulata, 28 Sept. 1952, *Acuña* 18222 (SV, HOLOTYPE; fruiting); banks of a rivulet, cuabales, east of Loma Cajalbana, La Palma, Oct. 1952, *Acuña* (LS, MICH); La Cajalbana, junto a cañada, Camino de Sagua, 12 Mar. 1954, *Acuña & Schubert* 19120 (GH, PARATYPE; male and female flowers).

This recently described species, which would still remain unknown were it not for the efforts of Ing. Julian Acuña, needs further study. Good material of the male flowers is sparse or lacking in most specimens of this and the other two species of sect. *Thamnocharis*, because the flowers appear

with the developing leaves and the male ones are soon deciduous. The androecium of *P. comptus* is of especial interest because of the apparently free filaments and the variable number of stamens. A count of 25 flowers yielded the following distribution (the first figure being the stamen number): 4 — 3, 5 — 9, 6 — 11, 7 — 1, 8 — 1. This range of variation nicely bridges the gap between the androecium of *P. discolor*, with 9–14 stamens, and the other two species of sect. *Thamnocharis*, with only 2. The presumption that *P. comptus* represents a phylogenetically important connecting link is thus strengthened.

Although there appears to be no serious doubt regarding the kinship of *P. comptus* with *P. cinctus* and *P. ekmanii*, the differences between the Pinar del Río and Oriente plants are so profound that their separation must be ancient; they could be placed in different subsections if there were any point in subdividing so small a section as *Thamnocharis*. The recognition of the hybridization between *P. comptus* and *P. discolor* (discussed in detail under the latter) has further complicated the picture. Although these two species obviously retain some degree of genetic compatibility, the cataphylls, leaves, styles, and seeds of *P. comptus* are so different from those of *P. discolor* that each species must represent the end-product of a long-separate evolutionary line. In common with several other species endemic to the Cajalbana area, *P. comptus* bears the earmarks of a relict species the nearest relatives of which have long since disappeared.

56. *Phyllanthus cinctus* Urb. Symb. Ant. 9: 191–192. 1924; emend. Webster, Contr. Gray Herb. 176: 60. 1955.

(PLATE XXVI, figs. D–F).

Conami (?) *ovalifolia* Britton, Mem. Torr. Bot. Club 16: 73–74. 1920; non *Phyllanthus ovalifolius* Forsk., 1775.

Phyllanthus brittonii Alain, Contr. Mus. La Salle 11: 1. 1952.

Subshrub or shrub 0.15–1 m. high, with the habit of a miniature tree, the primary stem unbranched, greyish, furrowed, c. 4–8 mm. thick. Lower leaves (missing on many specimens) with petioles c. 5–7 mm. long, leaf-blades obovate or spatulate, 4–6.5 cm. long; upper leaves reduced to cataphylls: stipules triangular-lanceolate (somewhat falcate), acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad on weak axes), obliquely truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, somewhat blackish and glandular at the base, sometimes densely hirtello-scabridulous at the base or throughout, scarious-indurate; blade acicular, 7.5–9 mm. long. Deciduous branchlets erect to spreading, (10–) 15–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. (4–) 8–15 leaves; first internode (15–) 20–50 (–65) mm. long, median internodes (10–) 15–25 (–40) mm. long. Leaves: stipules caducous (represented in most specimens only by small scars), broadly lanceolate, c. 3.5–4 mm. long, acuminate, entire or obscurely denticulate, brownish, scarious. Petioles subterete (somewhat flattened adax-

ially), rugulose or sometimes scabridulous, 2.5–5 mm. long. Leaf-blades coriaceous, oblong-elliptic, tending to be slightly obovate, (3–) 4–8 cm. long, (1.5–) 2–3.5 (–4.5) cm. broad, obtuse or rounded and with a minute blackish apiculum (sometimes obsolete) at the tip, acute to obtuse at the base; above sublucid or dully olivaceous, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a somewhat prominent reticulum; beneath paler, the midrib prominently raised, the laterals (mostly 6–10 on a side) and veinlets forming a prominent reticulum; margins with a reflexed thickened marginal rim (which is colored as the rest of the undersurface).

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 (rarely 3) female and c. 10–12 male flowers.

Male flower: pedicel slender, 3–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, chartaceous, biseriate, the outer broadly ovate or oblong, the inner obovate or suborbicular, 1.9–2.1 mm. long, 1.4–2 mm. broad, rounded and entire at the tip, mostly 3-nerved, the irregular veins dark and conspicuous. Disk-segments 4, irregularly cubical or subglobose, foveolate-pitted, 0.4–0.6 mm. across. Stamens 2; filaments completely connate into a rather slender terete column usually 0.6–0.9 mm. high and 0.2–0.25 mm. thick; anthers erect, sessile atop the column, discrete or fused back-to-back below, triangular-ovate, (0.5–) 0.6–0.8 mm. long, 0.4–0.5 mm. broad; anther-sacs subparallel, dehiscing vertically, the slits not confluent; pollen grains c. 20–24 μ in diameter, areoles oligobrochate or transitional to polybrochate, c. 12–15 per amb, 4–6 μ across.

Female flower: pedicel terete and slender at the very base but abruptly dilated above, not angled, 4–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, coriaceous, biseriate, subequal or unequal, at anthesis more or less spreading with the tips reflexed, elliptic to broadly ovate-oblong, the larger lobes c. 3–5 (–6) mm. long and 2–4 (–5) mm. broad, rounded or obtuse at the tip, triplinerved but the laterals much less conspicuous than in the male calyx, mesophyll densely crystalliferous. Disk squarish, the 4 coalesced segments forming a shallow undulate-crenulate, foveolate-pitted cup c. 2 mm. across. Ovary reddish brown, sulcate, the tips of the carpels slightly projecting above the insertion of the styles; styles erect, 2.3–3.5 mm. high, connate into a comparatively slender column 1.7–2.4 mm. high and 0.4–0.55 mm. thick; stylar branches divergent, recurving, terete and narrowed to subacute tips.

Capsule obtusely angled, c. 5.5–6 mm. in diameter, smooth, reddish-brown, not veiny. Columella 2.5–3 mm. long. Seeds trigonous, symmetric, 3.7–4 mm. long, 2.4–2.8 mm. radially and tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, elliptic, c. 0.5 mm. long.

Collected flowering Feb.–Apr., Aug.; fruiting Feb.–Mar., July.

TYPE: Cuba, *Shafer 8446*.

DISTRIBUTION: serpentine areas, usually in pinelands, eastern Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE: Cananova, sur le charrascal serpentineux du Cerro de Miraflores, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain* 21634 (MT); vicinity of Moa, Arroyo Moa, 10 Apr. 1945, *Acuña* 12479 (SV, US); Moa, pinares, summer 1939, *Mrs. Bucher* 61 (NY, SV); Moa, río de la scierie, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain* 21635 (MT); Moa, 29 Aug. 1917, *Roig* 1545 (NY, SV); wet pinelands near Punta Gorda, 14 July 1947, *León & Clemente* 23057 (MICH); rich woods, alluvial valley of Río Yamanigüey, 27 Feb. to 1 Mar. 1910, *Shafer* 4228 (NY, US), 4274 (F, NY); between Yamurí Arriba and Bermejál, Feb. 1911, *Shafer* 8446 (NY, LECTOTYPE); Cuchillas de Baracoa, c. 1 mi. north of Río Yumurí, pinelands, alt. c. 2000 ft., 18 Mar. 1954, *Jervis* 3355 (GH).

Of the three species of sect. *Thamnocharis*, *P. cinctus* is the commonest and most widespread, occupying relatively mesophytic riparian habitats as well as drier pinelands or scrub. It correspondingly is the most variable of the three species, and *Jervis* 3355 is particularly divergent due to its large female calyx (the longer lobes being 6 by 5 mm. instead of 3–5 by 2–4 mm.) and smaller leaves with only 5–7 lateral veins. In these respects it partially closes the morphological gap between *P. cinctus* and *P. ekmanii* and provides additional support for the possible alternative course of grouping these plants as two subspecies of a single species. Nevertheless, the gap — although narrowed — remains, and until further knowledge of the range of variation can be obtained, the present arrangement appears to be the best.

Also occurring in the Moa region within the range of *P. cinctus* is the narrowly endemic *P. chryseus* (sect. *Glyptothamnus*), which is strikingly similar in its habit, tetramerous calyx and androecium of two stamens. However, it differs in so many important respects (e.g., persistent stipules, unisexual inflorescence, annular male disk, lacerate styles) that the similarity to *P. cinctus* would seem to be ascribable to convergent development rather than to a close affinity.

57. *Phyllanthus ekmanii* Webster, Contr. Gray Herb. 176: 60. 1955.
(PLATE XXVI, figs. G–J; PLATE XXVII, fig. B).

Phyllanthus cinctus Urb. Symb. Ant. 9: 191–192. 1924 (as to description, not as to type).

Subshrub or treelet, with the habit of *P. cinctus*, 0.3–1 m. high. Lower leaves of main axis (missing on many specimens) with petioles 5–7 mm. long, leaf-blades obovate or broadly elliptic, 3.5–6.5 cm. long and 2–4 cm. broad; upper leaves reduced to cataphylls: stipules triangular-lanceolate, acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad), truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, scarious-indurate; blade acicular. Deciduous branchlets erect to spreading, (8–) 10–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. 7–15 leaves; first internode 15–45 mm. long, median internodes 10–25 mm. long. Leaves: stipules cadu-

cous (represented in most specimens only by small scars), lanceolate, c. 1.5–2 mm. long, acuminate, obscurely denticulate, brownish, scarious. Petioles somewhat flattened adaxially, rugulose, sometimes scabridulous, (2–) 2.5–4 mm. long. Leaf-blades stiffly coriaceous, elliptic to slightly ovate, (2.5–) 3–5 (–6) cm. long, 1.3–3 (–3.5) cm. broad, obtusely rounded or emarginate at the tip (the minute blackish apiculum nearly or quite obsolete), cuneate to obtuse or rounded at the base; above sublucid, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a prominent somewhat raised reticulum; beneath paler, the midrib prominently raised, the lateral (c. 4–6 on a side) and tertiary veins forming a reticulum more prominent than that above; margins with a reflexed thickened brownish or somewhat orange marginal rim.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 female and c. 2–5 male flowers.

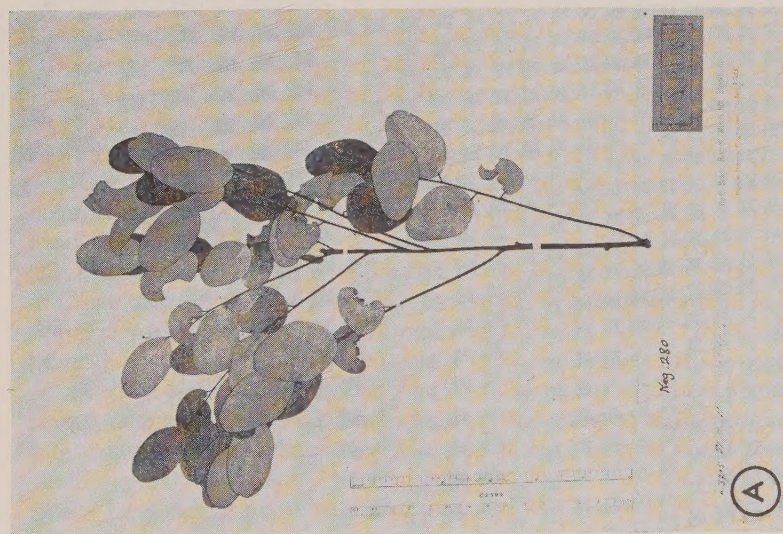
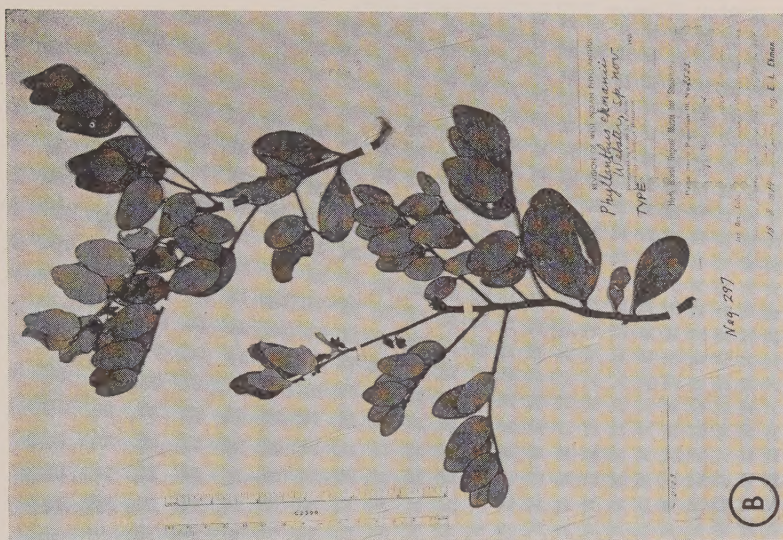
Male flower: pedicel slender, becoming 4–9 mm. long, abruptly dilated and fleshy above. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, chartaceous, biseriate, suborbicular, 3–3.7 mm. long, 2.3–2.7 (–3) mm. broad, rounded and entire at the tip, ordinarily with 5–7 nerves from the base but these not very conspicuous. Disk-segments 4, subrectangular, more or less flattened, rugulose, c. 0.7–1.1 mm. across. Stamens 2; filaments completely connate into a stout column c. 0.5–0.8 mm. high and 0.6 mm. thick; anthers erect, sessile atop the column, fused back-to-back from $\frac{1}{3}$ to all their lengths, narrowly triangular-lanceolate, c. 1–1.2 mm. long, 0.5–0.7 mm. broad; anther-sacs slightly divergent, dehiscing vertically, the slits not confluent; pollen grains c. 24–28 μ in diameter, areoles oligobrochate, mostly 15–18 per amb, c. 4–6 μ across.

Female flower: pedicel terete and slender at the base but abruptly dilated above, not angled, 2.5–5 (–6) mm. long. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, coriaceous, biseriate, subequal, broadly ovate or elliptic (the outer strongly convex, the inner conduplicate), erect (the tips not reflexed), the larger lobes 6–8 mm. long and 3–5 mm. broad, rounded at the tip, with c. 6 or 7 subparallel conspicuously reticulate-ramifying nerves, mesophyll densely crystalliferous. Disk squarish, very massive, forming below the ovary a mound-like pedestal c. 0.5–1 mm. high and 3–4 mm. broad, the foveolate rim depressed.

Ovary reddish brown, strongly sulcate; styles erect, 3–5 mm. high, connate into a column (2.1–) 2.5–4 mm. high and c. 0.4 mm. thick (somewhat dilated upwards); stylar branches divergent, slender, recurving, terete and narrowed to subacute tips.

Capsule valves c. 5 mm. long, reddish brown, smooth, not veiny. Columella nearly 3 mm. long. Seeds trigonous, nearly symmetric, 3.3–3.4 mm. long, 2–2.2 mm. radially, 2.2–2.5 mm. tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, ovoid or elliptic, c. 0.5 mm. long.

Collected flowering Feb., Apr., Aug.; fruiting May, June, July.



GROWTH FORM IN SECTS. *Williamia* AND *Thamnocharis*. FIG. A. *Phyllanthus microdictyus* Urb. (*Ekman* 3705 [S, HOLOTYPE]). FIG. B. *Phyllanthus ekmanii* Webster (*Ekman* 2523 [S, HOLOTYPE]); note the unreduced leaves on the lower part of the main axis.

TYPE: Cuba, *Ekman* 2523.

DISTRIBUTION: restricted to serpentine areas of the Sierra de Nipe, Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE, SIERRA DE NIPE: Cayo del Rey, Pinar Colorado, 16 Apr. 1940, *Carabia* 3587 (MICH, NY); Río Piloto, locis rupestribus, alt. 750 m., 18 Aug. 1914, 15 May 1915, *Ekman* 2523 (S, HOLOTYPE; NY, ISOTYPE), 5704 (S); charrascales, Río Piloto, 10 June 1915, 27 Apr. 1919, *Ekman* 6026, 19166 (S); charrascales, ad viam Bio, 27 Apr. 1919, *Ekman* 9583 (S); exposed ridge, Pico Estrella, 18 Feb. 1954, *Jervis* 3037, 3065 (GH).

This species endemic to the Sierra de Nipe is so closely related to *P. cinctus* that Urban's confusion (in associating specimens of the former with the name of the latter) is understandable. Although some of the distinctions between the two taxa are not quite absolute and may even further break down upon study of additional collections, there are so many points of difference that it seems preferable to rank them as closely related allopatric species rather than as two subspecies of one variable species. The larger size of the male flower, at least, always distinguishes *P. ekmanii*; and its hypertrophied female disk, which somewhat recalls the gynophore of *P. microdictyus*, is very different from the unmodified disk of *P. cinctus*. In addition, the female calyx and styles of *P. ekmanii* appear to be definitely larger than those of *P. cinctus*, but the dimensions of these organs are subject to such variation after anthesis that on the basis of specimens at hand it is difficult to make comparable measurements. There are, furthermore, additional differences in the mean values of such characters as leaf-size and vein-number which lend support to the supposition that *P. ekmanii* and *P. cinctus* are distinct species.

In contrast to *P. cinctus*, which ranges over much of the Sagua-Baracoa massif, *P. ekmanii* has a much more restricted range; it has thus far been collected only in the southern part of the Sierra de Nipe but not in the vicinity of Loma Mensura or Bandera. The only divergent specimen noticed was *Jervis* 3037 which, according to the collector, had "creamy-white" rather than reddish flowers. Unfortunately no flowers were present on the single available specimen of this collection number; but since *Jervis* 3065 from the same locality has typically reddish flowers, it would appear that the whitish-flowered form is only a trivial local variant.

(To be concluded)